Global Effects of Feature-based Attention Depend on Surprise

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Abstract

Recent studies have shown that prediction and attention can interact under various circumstances, suggesting that the two processes are based on interdependent neural mechanisms. Attention is broadly used to describe a number of subcomponents, however, and it remains unclear which of these mechanisms interacts with prediction and in what manner. In particular, it is currently unknown whether prediction can interact with feature-based selection outside the current spatial focus of attention. Here, across two experiments, we recorded neural activity with electroencephalography (EEG) as human observers performed a feature-based attention task at fixation and ignored a stream of peripheral stimuli with predictable or surprising features. Central targets were defined by a single feature (colour or orientation) and differed in salience across the two experiments. Task-irrelevant peripheral patterns usually comprised one particular conjunction of features (standards), but occasionally deviated in one or both features (deviants). Consistent with previous studies, we found main effects of feature-based attention and prediction on neural responses to task-irrelevant patterns in both experiments. Crucially, we observed an interaction between the effects of prediction and feature-based attention in both experiments: neural responses to surprising but not predictable patterns were modulated by feature-based attention. These findings suggest that global effects of feature-based attention depend on surprise, and are consistent with the idea that attention optimises the precision of predictions by modulating the gain of prediction errors.

Introduction

Selective attention mechanisms enhance the processing of sensory stimuli that are relevant for guiding behaviour (Desimone & Duncan, 1995; Posner, 1994). Visual processing can be biased toward stimuli at a relevant location, commonly known as 'spatial attention', or toward stimuli that possess task-relevant features, known as 'feature-based attention' (Carrasco, 2011). Monkey neurophysiology studies (Martinez-Trujillo & Treue, 2004) and human neuroimaging studies (Gledhill, Grimsen, Fahle, & Wegener, 2015; Saenz, Buracas, & Boynton, 2002; Serences & Boynton, 2007) have demonstrated that neural responses to stimuli at task-irrelevant locations are enhanced when they possess task-relevant features, demonstrating that the effects of feature-based attention are global and dissociable from those of spatial attention. In humans, neural responses to visual stimuli at task-irrelevant locations can be enhanced when they possess surprising features (e.g., colour, orientation, motion), demonstrating that top-down 'prediction' mechanisms also exert a global effect on incoming sensory signals (Friston, 2005; Stefanics, Kremlácek, & Czigler, 2014). At present, it is unknown whether the global effects of visual feature-based attention can interact with those of prediction. Here we used electroencephalography (EEG) to measure neural responses to peripheral visual stimuli that were predictable or surprising along two feature dimensions (orientation and colour), and tested whether attending to a particular feature at fixation modulated the effect of prediction on neural responses to peripheral stimuli at task-irrelevant locations.

Predictive coding theories propose that top-down prediction signals silence bottom-up sensory signals that match the predicted content, leaving only the remaining *prediction error* to propagate forward and update a model of the sensory environment (Friston, 2005; Rao & Ballard, 1999). In addition to predicting the *content* of sensory signals, an optimal inference system should also estimate the level of uncertainty about its predictions (i.e., inverse precision;

Hohwy, 2012). Recently, it has been proposed that mechanisms of selective attention fulfil this role, optimising the expected precision of predictions by enhancing the activity of units encoding prediction errors for attended stimuli (Feldman & Friston, 2010; Friston, 2009, 2010). Recent studies have supported this theory by demonstrating that selective attention and prediction can interact under various circumstances (Auksztulewicz & Friston, 2015; Jiang, Summerfield, & Egner, 2013; Kok, Rahnev, Jehee, Lau, & De Lange, 2012; Marzecová, Widmann, SanMiguel, Kotz, & Schröger, 2017; Smout, Tang, Garrido, & Mattingley, 2019). However, selective attention mechanisms encompass various information-processing subcomponents (e.g. spatial attention, temporal attention) across sensory modalities (e.g., auditory, visual) and it is important to establish which of these subcomponents interact with prediction and in what manner. In the visual domain, previous studies that reported an interaction between attention and prediction typically presented stimuli at task-relevant locations (Jiang et al., 2013; Kok, Rahnev, et al., 2012; Marzecová et al., 2017; Smout et al., 2019). One previous study found an effect of feature-based attention on mismatch responses to stimuli at task-irrelevant locations, but this study presented clearly visible targets that likely did not necessitate a tight focus of spatial attention to the central stimulus stream (Czigler & Sulykos, 2010). Thus, it remains unclear whether prediction can interact with global feature-based attention mechanisms that modulate neural responses to stimuli outside the spatial focus of attention.

Here, we tested whether feature-based attention modulates the effect of prediction at task-irrelevant locations by comparing event-related potentials evoked by peripheral stimuli that either matched ('congruent') or mismatched ('incongruent') the cued feature of the target at fixation. Participants searched for targets at fixation while predictable or surprising task-irrelevant stimuli were presented in the periphery. We conducted two experiments that differed

in the salience of central targets and distractors to investigate whether the strength of the top-down feature set modulates the neural interaction between feature-based attention and prediction.

Methods

Experiment 1: Effects of feature-based attention at fixation on neural responses to predicted and surprising peripheral stimuli

Participants

Twenty-four healthy adults (13 female, 11 male, age = 22.08 ± 2.38 years) with normal or corrected-to-normal vision were recruited for participation via an online portal at The University of Queensland. The study was approved by The University of Queensland Human Research Ethics Committee, and all participants provided written, informed consent before commencing the experiment.

Stimuli and apparatus

Participants were positioned at a viewing distance of 57 cm and seated in a comfortable armchair in an electrically shielded laboratory. Stimuli were presented on a 61 cm LED monitor (Asus, VG248QE) with a 1920 x 1080 pixel resolution and refresh rate of 120 Hz, using PsychToolbox presentation software (Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, 2007) for Matlab (v.15b) running under Windows 7 with an NVidia Quadro K4000 graphics card. The intensity of the green phosphor was adjusted per participant to produce subjective equiluminance with that of the red phosphor at full intensity. The equiluminance point was determined prior to the experiment using minimum motion photometry (Anstis & Cavanagh, 1983), with intensity values determined by two interleaved adaptive staircases (1 up-1 down, stopping after 15 reversals).

Central and peripheral stimuli were sinusoidal Gabors (diameter: 4.72˚, spatial frequency: 0.94 c/˚, 100% contrast) with one of two orientations (tilted 45° clockwise or counterclockwise of vertical) and one of two colours (red or green). Central stimuli were superimposed over a red-green noise patch (diameter: 4.72) and onset every 700 - 1400 ms for 66.67 ms. 20% of central stimuli were targets (approximately 28 targets and 114 distractors per block). Multi-element peripheral stimuli ('patterns') were arranged in three concentric circles (radii: 4.72°, 8.49°, 12.26°; containing 8, 14, and 20 Gabors, respectively; *Figure 1A*). Peripheral patterns were presented every 350 ms for 66.67 ms (428 events per block) on top of a background that alternated between uniform red and green pixels at the screen refresh rate (120 Hz), producing a subjective percept of a uniform brown background. During each block, peripheral patterns were more likely to contain one of the four possible feature conjunctions (e.g. clockwise-tilted red Gabors; 76% of presentations, *standards*), with the other three feature conjunctions equally likely (8% each, *deviants*). Standards were pseudo-randomized across blocks, and the order of deviants was pseudo-randomized within blocks.

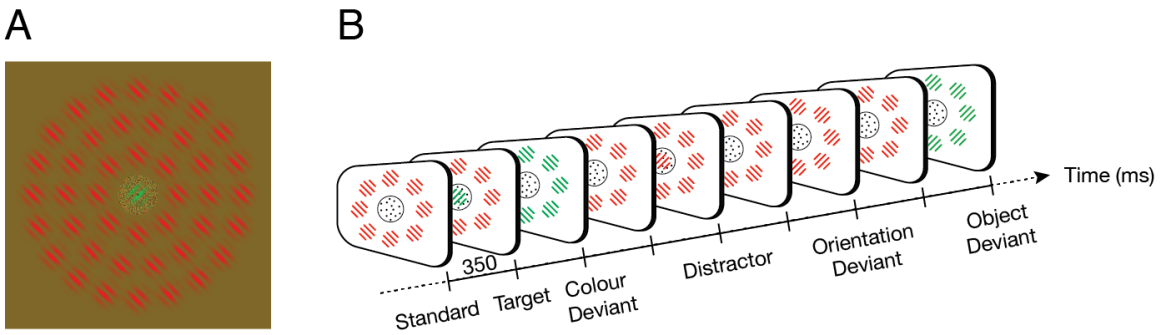

Figure 1. Stimulus display and task. (**A**) Stimulus display, showing a green clockwise-tilted target within the central noise patch and a peripheral pattern consisting of three concentric rings of red counterclockwise-tilted Gabors. (**B**) Simplified task diagram. In this example trial, participants searched for green Gabors (targets) and ignored red Gabors (distractors) within the central noise patch. Peripheral patterns typically contained red counterclockwise-tilted Gabors (standards), but occasionally contained red clockwise-tilted Gabors (orientation deviant), green counterclockwise-tilted Gabors (colour deviant), or green clockwise-tilted Gabors (object deviant, i.e. deviating in both colour and orientation). In this example trial, the colour and object deviants shared features with the target (i.e., green) and would thus be labelled 'congruent'.

Procedure

Participants were asked to fixate on a central dot and click a mouse button as soon as they detected a target in the stream of central stimuli, continuously throughout blocks (duration: 150 s), while ignoring central distractors and peripheral patterns (*Figure 1B*). In each block, Gabor targets were designated as either (1) red, (2) green, (3) clockwise-tilted, or (4) counterclockwise-tilted. Note that each condition dictated two of the four possible feature conjunctions as targets and two as distractors (e.g., if searching for clockwise-tilted targets, both red and green clockwise-tilted Gabors were valid targets).

Participants completed two practice blocks with auditory feedback after each response, before being fitted with the EEG cap and electrodes (see *EEG Data Acquisition*). Participants then completed 16 test blocks with target type and standard pattern features pseudorandomized across blocks (6848 peripheral patterns per session). Feedback on mean reaction time and the number of hits and false alarms was provided between blocks.

Behavioural Data Analysis

We investigated whether the feature-congruence and predictability of peripheral patterns affected participants' detection of central targets. Targets were sorted into *prediction conditions* according to whether the preceding pattern (i.e., the peripheral stimulus presented up to 700 ms prior to peak target contrast) was a standard ('predicted') or a deviant ('surprising'), and *feature-congruence conditions* according to whether the preceding peripheral pattern matched the features of the central target ('congruent') or distractor ('incongruent'). Participant responses were scored as hits if they occurred within 1 s of the onset of a target. Successive responses within this window were ignored, as were any responses that occurred within 250 ms of a preceding response. Because we observed differences in hit

rates and reaction times between target feature conditions (i.e., the feature that participants searched for at fixation, e.g. 'red'), we first normalised hit rates and reaction times within each target feature condition, separately for feature-congruence and prediction conditions, and then collapsed across the target feature conditions. The resulting normalised hit rates and reaction times were then subjected to two-way repeated measures ANOVAs to assess the effects of peripheral pattern prediction (two levels: predicted, surprising) and feature-congruence (two levels: congruent, incongruent) on target detection.

EEG Data Acquisition

Participants were fitted with a 64 Ag-AgCl electrode EEG system (BioSemi Active Two: Amsterdam, Netherlands). Continuous data were recorded using BioSemi ActiView software (http://www.biosemi.com), and were digitized at a sample rate of 1024 Hz with 24-bit A/D conversion and a .01 – 208 Hz amplifier band pass. All scalp electrode offsets were adjusted to below 20μV prior to beginning the recording. Pairs of flat Ag-AgCl electro-oculographic electrodes were placed on the outside of both eyes, and above and below the left eye, to record horizontal and vertical eye movements, respectively.

EEG Preprocessing

EEG recordings were processed offline using the EEGlab toolbox in Matlab (Delorme & Makeig, 2004). Data were resampled to 256 Hz and high-pass filtered with a passband edge at 0.5 Hz (1691-point Hamming window, cut-off frequency: 0.25 Hz, -6 db). Raw data were inspected for the presence of faulty scalp electrodes (none were found). To clean the data, we applied an iterative process of artifactual epoch and component rejection using independent component analyses (ICA). The data were segmented into 350 ms epochs surrounding Gabor onsets (50 ms pre- and 300 ms post-stimulus) and baseline activity prior to stimulus onset was

removed from each epoch. Epochs were subjected to ICA, and the SASICA plugin for EEGlab (Chaumon, Bishop, & Busch, 2015) was used to identify blink, saccade, and focal trial components. Epochs were rejected if they met any of the following criteria: (1) blink component activity greater than ±10 μV between -50 and 150ms; (2) saccade component activity greater ±5 μV between 0 and 350 ms; (3) focal component activity exceeding a joint probability threshold of ±7 SD (5.5% of epochs were removed due to blink, saccade, or focal activity). The remaining epochs were then subjected to ICA for a second time, and SASICA was used to identify artifactual components.

For further analysis, the resampled raw data were band-pass filtered between 0.5 and 40 Hz (1691-point Hamming window, cut-off frequencies: 0.25 and 40.25 Hz, -6 db) and segmented into 550 ms epochs surrounding Gabor onsets (100 ms pre- and 450 ms post-stimulus). Epochs containing artefacts (identified previously using the first ICA) were removed. Independent component weights from the second ICA were applied to this new dataset and previously identified artefactual components were removed. Baseline activity in the 100 ms prior to stimulus onset was removed from each epoch.

Event-Related Potential and Bayes Factor Analyses

Peripheral patterns were sorted into prediction conditions based on whether they were standards (repeated at least 4 times; 'predicted') or deviants ('surprising'), and attention conditions based on whether they shared features with central targets ('congruent') or distractors ('incongruent') in the central task. Trials in each attention and prediction condition were averaged within participants to produce event-related potentials (ERPs) for each individual. Statistical analyses of condition ERPs were conducted using two-tailed cluster-based permutation tests across participants (Monte-Carlo distribution with 5000 permutations,

200 $p_{cluster}$<0.05; sample statistic: dependent samples *t*-statistic, aggregated using the maximum
201 sum of significant adjacent samples, p_{sample}<.05) in the Fieldtrip toolbox for Matlab
202 (Oostenveld, Fries, Maris, & Schoffelen, 2011). Statistical analyses of univariate condition
203 averages were conducted using paired-samples *t*-tests and Bayesian analyses. Bayes factor
204 analyses allow for quantification of evidence in favour of either the null or alternative
205 hypothesis, with $BF_{10} > 3$ indicating substantial support for the alternative hypothesis and BF_{10}
206 < 0.33 indicating substantial support for the null hypothesis. Bayes factors were computed
207 using the Dienes (2014) calculator in Matlab.

208 **Experiment 2: Replication with individually thresholded manipulation of feature-based**
209 **attention at fixation**

210 In Experiment 1, the high contrast targets were detected at near-ceiling levels. To investigate
211 whether the neural interaction between feature-based attention and prediction is sensitive to the
212 strength of the top-down feature set, we conducted a second experiment in which central targets
213 and distractors were individually thresholded to be less salient. Except for the differences noted
214 below, the methods used in Experiment 2 were the same as those described for Experiment 1.

215 *Methods*

216 A new cohort of 24 healthy adults with normal (or corrected-to-normal) vision was recruited
217 to participate in Experiment 2 (12 female, 12 male, age = 22.17 ± 2.88 years, mean ± SEM).
218 The stimuli and apparatus were identical to those used in Experiment 1 (*Figure 1*), except that
219 in Experiment 2 the central stimuli (targets and distractors) were presented at lower contrast
220 and with a sinusoidal onset and offset profile (total duration: 700 ms). The peak contrast of the
221 central stimuli was determined during the two practice blocks, using a transformed and
222 weighted up/down adaptive staircase configured to approximate 83% detection of targets

(up/down step ratio: 1/3, up/down size ratio: .1/.07; García-Pérez, 1998). Blocks lasted for 150 s (as per Experiment 1) for all except two participants, for whom blocks lasted for 120 s (due to time constraints for these two individuals). Participant responses were scored as hits if they occurred within 1 s of the peak target contrast (i.e. within 1.35 s of target onset, accounting for the 350 ms on-ramp). During EEG preprocessing, we interpolated 11 faulty electrodes (across 5 participants) using the average activation across neighbouring electrodes (defined by the EEGlab Biosemi 64 template) and removed 4.1% of epochs due to blink, saccade, or focal component contamination.

Results

Experiment 1: Effects of feature-based attention at fixation on neural responses to predicted and surprising peripheral stimuli

Feature-Congruent Peripheral Patterns Interfere with Target Detection at Fixation

We investigated whether the congruence between peripheral pattern and central target features affected the detection of central targets shortly after pattern onset. We observed a significant main effect of feature-congruence on normalised reaction times, with participants responding more slowly to central targets preceded by congruent peripheral patterns (438.80 ± 9.43 ms, mean ± SEM; 0.04 ± 0.19 z-normalised) than to central targets preceded by incongruent peripheral patterns (436.09 ± 9.53 ms; -0.04 ± 0.20 z-normalised, $F(1,23) = 5.70$, $p = .026$, $\eta_p^2 = 0.20$). There was no main effect of feature-congruence on normalized hit rates (congruent = 94.41 ± 1.28%, 0.06 ± 0.19 z-normalised, incongruent = 93.63 ± 1.39%, -0.08 ± 0.20 z-normalised, $F(1,23) = 3.33$, $p = .081$, $\eta_p^2 = .013$).

Peripheral Pattern Prediction Does Not Affect Target Detection

We were also interested in whether the predictability of peripheral patterns affected behavioural responses to subsequent central targets. We found no effect of peripheral pattern prediction on normalised hit rates (predicted = 94.39 ± 1.22%, 0.04 ± 0.18, surprising = 93.65 ± 1.47%, -0.06 ± 0.21, $F(1,23) = 1.63$, $p = .215$, $\eta_p^2 = .07$) or normalised reaction times (predicted = 437.12 ± 9.66 ms, -0.01 ± 0.20, surprising = 437.76 ± 9.32 ms, 0.01 ± 0.19, $F(1,23) = 0.27$, $p = .605$, $\eta_p^2 = .01$). There was also no interaction between prediction and feature-congruence on either normalised hit rates ($F(1,23) = 0.31$, $p = .582$, $\eta_p^2 = .01$) or normalised reaction times ($F(1,23) = 0.15$, $p = .701$, $\eta_p^2 = .01$).

Prediction Decreases Neural Activity

We assessed the main effect of prediction on neural activity by comparing ERPs to peripheral deviant patterns ('surprising' patterns, collapsed across orientation, colour, and object deviants) and standard patterns that had been repeated at least 4 times ('predicted' patterns). Relative to baseline, standards evoked smaller neural responses than deviants (*Figure 2*). Over posterior electrodes, the neural response to standards was significantly reduced relative to deviants during both the early negative deflection (i.e. standards > deviants; 82 - 164 ms, $p = .020$) and the late positive deflection (i.e. standards < deviants; 242 – 348 ms, $p = .010$; *Figure 2B*). Over frontal electrodes, the neural response to standards was significantly reduced relative to deviants during both the early positive deflection (i.e. standards < deviants; 90 - 230 ms, $p < .001$) and the late negative deflection (i.e. standards > deviants; 254 – 348 ms, $p = .008$; *Figure 2A*). These effects are consistent with the theory that surprising stimuli (deviants) produce greater prediction errors than predicted stimuli (standards; Friston, 2005, 2009; Rao & Ballard, 1999).

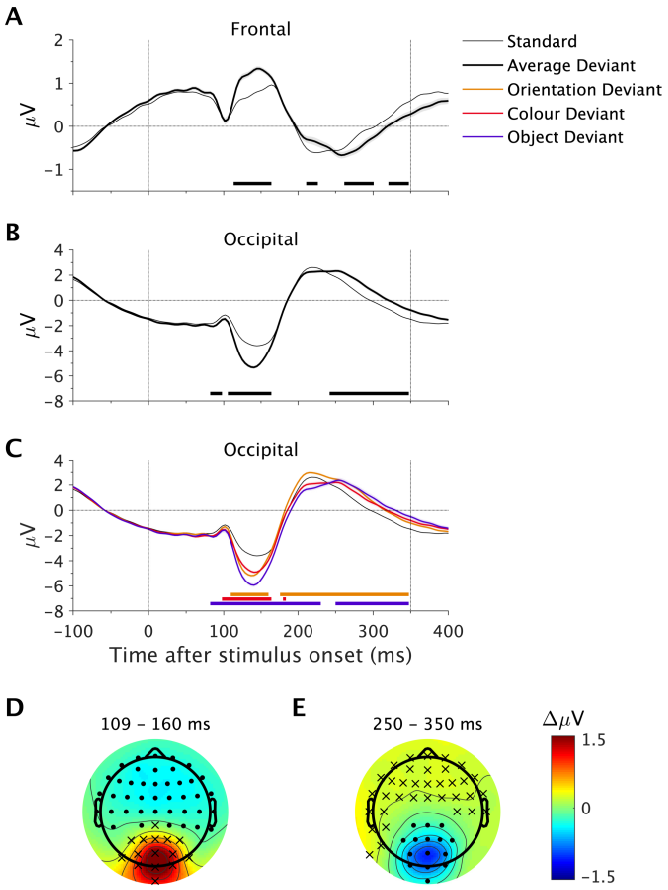

Figure 2. Main effect of prediction in Experiment 1. **(A-B)** ERPs evoked by standards and deviants (collapsed across deviant types) at frontal electrodes (Fz, F1, F3, AFz, AF3, AF4; **A**) and occipital electrodes (Oz, O1, O2, POz, PO3, PO4; **B**). Shading indicates the within-subject standard error of the mean, calculated relative to standards. Black bars along the x-axis denote significant timepoints at the displayed electrodes (cluster-corrected). (**C**) ERPs evoked by standards and each of the three deviant conditions. Shading indicates the within-subject standard error of the mean, calculated separately for each deviant condition relative to standards. Yellow, red and purple bars along the x-axis denote significant differences between standards and each corresponding deviant condition (cluster-corrected). (**D-E**) Headmaps show the effect of prediction (standard minus average deviant) during the indicated time windows. Asterisks and dots denote electrodes with larger or smaller responses, respectively, across at least 33% of the averaged time points (cluster-corrected).

We followed up this result with direct comparisons between standards and each type of deviant, which revealed similar effects to those reported above for the average deviant condition (*Figure 2C*). Early posterior negativities were smaller in response to standards than orientation deviants (109 – 160 ms, $p = .033$), colour deviants (98 – 164 ms, $p = .040$), and object deviants (82 – 348 ms, $p < .001$), and late posterior positivities were significantly smaller in response to standards than orientation deviants (176 – 348 ms, $p < .001$) and object deviants (250 – 348

ms, $p = .019$). Early frontal positivities were smaller in response to standards than orientation deviants (98 – 164 ms, $p = .002$), colour deviants (86 – 238 ms, $p = .001$), and object deviants (102 – 238 ms, $p < .001$), and late frontal negativities were smaller in response to standards than orientation deviants (242 – 348 ms, $p < .001$) and object deviants (84 – 348 ms, $p < .001$).

Visual Mismatch Negativities Are Additive Across Feature Deviations

Because previous investigations have suggested that the visual mismatch negativity (vMMN) is non-additive across feature deviations (Czigler & Sulykos, 2010), we also tested for differences between vMMNs evoked by each type of deviant (orientation, colour, or object). We used a data-driven approach to identify spatiotemporal samples (electrodes x timepoints) that were significantly different from standards in all three deviant conditions (electrodes: Pz, P1, P2, P3, P4, POz, PO3, PO4, Oz, O1, O2, Iz; timepoints: 109 – 160 ms) and then averaged across these samples to produce one amplitude value per deviant condition and participant. We then compared each pair of deviant conditions with paired-samples *t*-tests and Bayesian analyses, using a uniform prior with upper and lower bounds set to the average vMMN amplitude. As can be seen in *Figure 2C*, there was no difference between the orientation (-1.02 ± 0.13 μV) and colour vMMN (-0.98 ±Z0.14 μV, $t(23) = -0.35$, $p = .733$, $BF_{10} = 0.14$). The object vMMN (-1.64 ± 0.16 μV) was significantly larger than both the orientation ($t(23) = -5.39$, $p < .001$, $BF_{10} > 10{,}000$) and colour vMMN ($t(23) = -7.06$, $p < .001$, $BF_{10} > 10{,}000$), however, suggesting that the vMMN is sensitive to features of the deviant stimulus.

Feature-based Attention Decreases Neural Activity

We assessed the main effect of feature-based attention by comparing ERPs to peripheral patterns that shared features with targets ('congruent') or distractors ('incongruent') in the central detection task. Congruent peripheral patterns evoked a smaller positivity over posterior

electrodes than incongruent patterns late in the epoch (188 – 305 ms, p = .004; *Figure 3B,D*). This effect was matched by a polarity-reversed activity profile over frontal electrodes (191 – 309 ms, p = .003; *Figure 3A,D*).

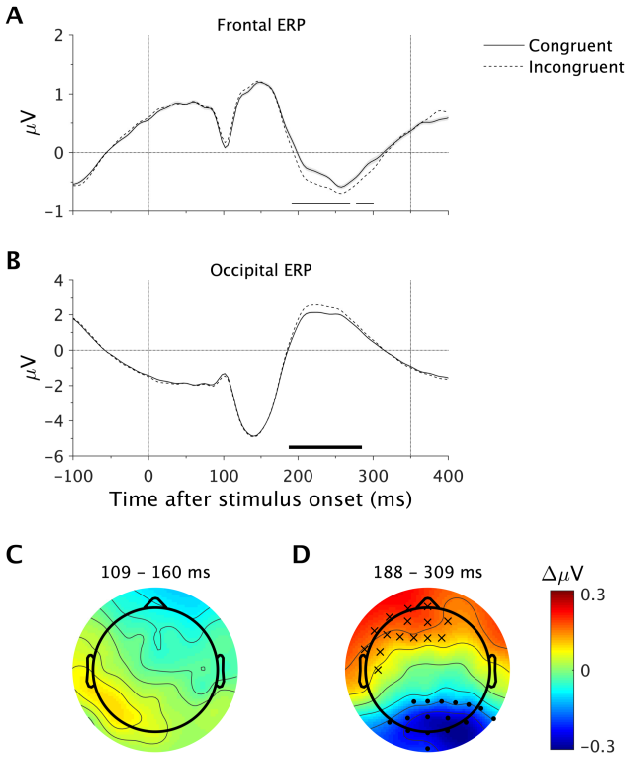

Figure 3. Main effect of feature-based attention in Experiment 1. (**A**-**B**) Congruent and incongruent ERPs are collapsed across prediction conditions separately for frontal electrodes (Fz, F1, F3, AFz, AF3, AF4; **A**) and occipital electrodes (Oz, O1, O2, POz, PO3, PO4; **B**). Shading indicates the within-subject standard error of the mean. Black bars along the x-axis denote significant differences at the displayed electrodes (cluster-corrected). (**C**-**D**) Headmaps show the effects of feature-based attention (congruent minus incongruent) during the indicated time windows. Asterisks and dots denote electrodes with larger, or smaller responses, respectively, in at least 33% of the averaged time points (cluster-corrected).

The Effect of Feature-based Attention Depends on Surprise

Next, we investigated the interaction between feature-based attention and prediction by subtracting the standard ERP from the deviant ERP (i.e., the mismatch response, collapsed across deviant conditions) and comparing difference waves between congruent and incongruent conditions (*Figure 4*). Over posterior electrodes, the mismatch response was more

negative for congruent stimuli than incongruent stimuli late in the epoch (203 – 285 ms, p = .041; *Figure 4B*). Inspection of individual condition ERPs (*Figure 4E*) revealed that posterior responses to deviants were reduced with feature-based attention, but responses to standards were unchanged.

We followed up this finding by averaging spatiotemporal samples spanned by the significant effect, separately for each deviant condition. We then compared congruent and incongruent conditions with paired t-tests and Bayesian analyses (uniform prior with upper and lower bounds set to the average amplitude across all conditions). Feature-based attention decreased the mismatch response to all three deviant types (orientation: congruent = 0.13 ± 0.10 μV, incongruent = 0.42 ± 0.13 μV, $t(23) = -2.16$, $p = .041$, $BF_{10} = 1.18$; colour: congruent = -0.45 ± 0.17 μV, incongruent = 0.05 ± 0.14 μV, $t(23) = -3.28$, $p = .003$, $BF_{10} = 1.41$; object: congruent = -0.53 ± 0.19 μV, incongruent = -0.06 ± 0.14 μV, $t(23) = -2.92$, $p = .008$, $BF_{10} = 1.28$; *Figure 4C*).

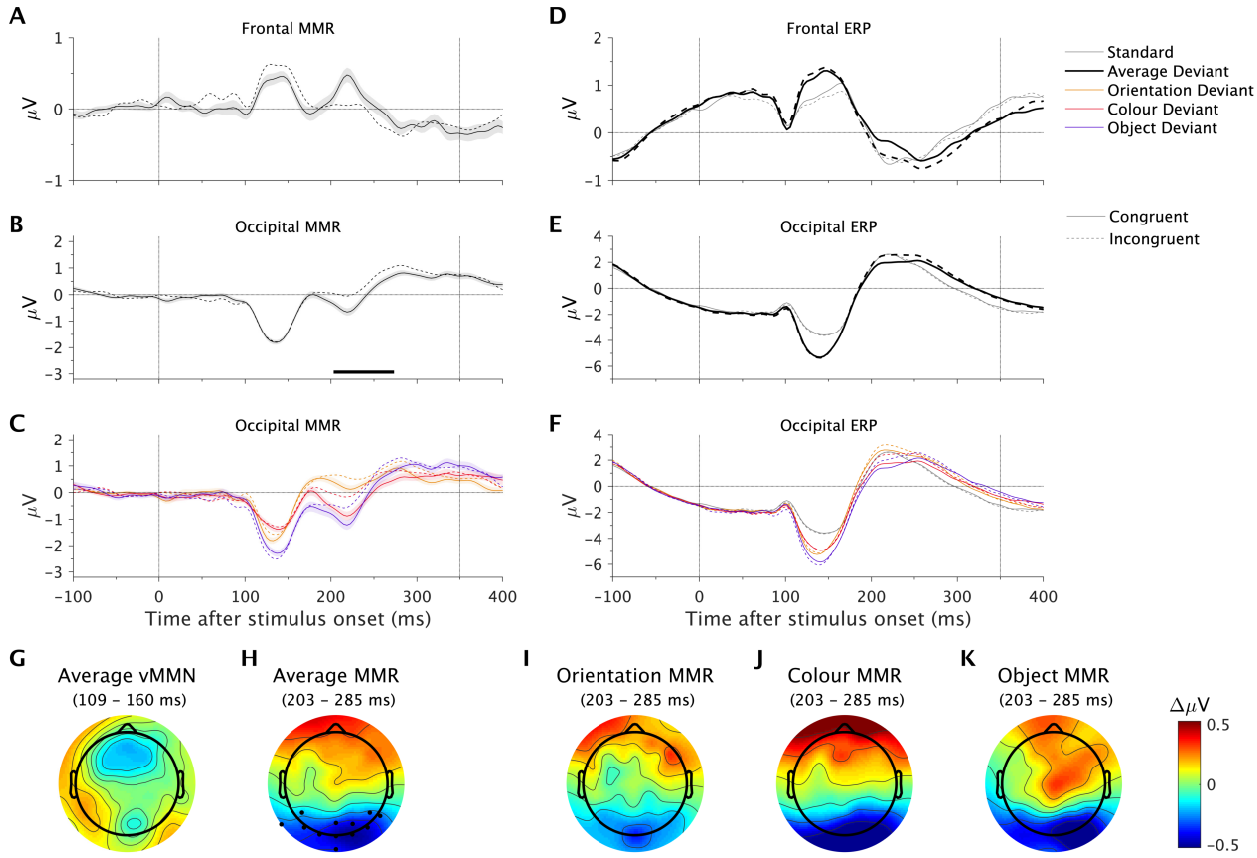

Figure 4. Interaction between feature-based attention and prediction in Experiment 1. (**A**-**B**) Average mismatch response (MMR; average deviant minus standard) collapsed across frontal electrodes (Fz, F1, F3, AFz, AF3, AF4; **A**) and occipital electrodes (Oz, O1, O2, POz, PO3, PO4; **B**). Solid lines represent the congruent condition and dotted lines represent the incongruent condition. Shading indicates the within-subject standard error of the mean. The black bar along the x-axis denotes significant differences at the displayed electrodes (cluster-corrected). (**C**) Mismatch responses at occipital electrodes for individual deviant conditions. (**D**-**E**) ERPs evoked by standards and deviants (averaged across deviant types), shown separately for congruent (solid) and incongruent (dotted) conditions. (**F**) ERPs for individual deviant conditions, shown separately for congruent (solid) and incongruent (dotted) conditions. (**G**-**H**) Headmaps show the effect of feature-based attention (congruent minus incongruent) on the average deviant mismatch response (average deviant minus standard) during the early vMMN (**G**) and late interaction time windows (**H**). Dots denote electrodes with significant differences in at least 33% of the averaged time points (cluster-corrected). (**I**-**K**) Effect of feature-based attention (congruent minus incongruent) on the orientation mismatch response (**I**), colour mismatch response (**J**) and object mismatch response (**K**) during the late interaction time window. Note that cluster-based permutation tests were not conducted on these differences.

The Visual Mismatch Negativity is Not Modulated by Feature-based Attention

Because previous literature has provided evidence for an effect of feature-based attention on the vMMN (Czigler & Sulykos, 2010), we also used Bayes analyses to test for differences between congruent and incongruent conditions during the (non-significant) vMMN time

359 period. Spatiotemporal samples spanning the common vMMN window (electrodes: Pz, P1, P2,
360 P3, P4, POz, PO3, PO4, Oz, O1, O2, Iz; timepoints: 109 – 160 ms) were averaged to produce
361 one amplitude value for each condition within participants. Congruent and incongruent
362 conditions were compared within deviant conditions using paired-samples *t*-tests and Bayes
363 analyses (uniform prior with upper and lower bounds set to the average amplitude across
364 conditions). We found no difference between congruent and incongruent vMMNs for any
365 deviant type (orientation: congruent = -1.09 ± 0.13 μV, incongruent = -0.95 ± 0.16 μV, $t(23)$ =
366 -1.23, p = .231, BF_{10} = .26; colour: congruent = -1.00 ± 0.16 μV, incongruent = -0.96 ± 0.14
367 μV, $t(23)$ = -0.37, p = .713, BF_{10} = 0.13; object: congruent = -1.55 ± 0.19 μV, incongruent = -
368 1.73 ± 0.15 μV, $t(23)$ = 1.29, p = .208, BF_{10} = 0.33; *Figure 4C*).

369 **Experiment 2: Replication with individually thresholded manipulation of feature-based**
370 **attention at fixation**

371 *Peripheral Patterns Do Not Modulate Behaviour in a Demanding Feature-based Attention*
372 *Task*

373 We investigated whether behavioural responses to low contrast targets in Experiment 2, which
374 necessitated a stronger top-down feature set than the high contrast targets in Experiment 1,
375 were affected by the predictability and feature-congruence of immediately preceding peripheral
376 patterns. In contrast to Experiment 1, we found no effect of feature-congruence on normalised
377 reaction times in Experiment 2 (congruent: 391.79 ± 11.12 ms, -0.01 ± 0.18 z-normalised;
378 incongruent: 392.49 ± 11.56 ms, 0.02 ± 0.18 z-normalised; $F(1,23)$ = 1.00, p = .329, η_p^2 = .04),
379 suggesting that the strength of the top-down feature set modulates the effect of congruent
380 patterns on target detection. In line with Experiment 1, all other behavioural effects were non-
381 significant. There was no effect of feature-congruence on normalised hit rates (congruent =
382 74.90 ± 2.05%, -0.02 ± 0.16 z-normalised, incongruent = 75.23 ± 2.14%, 0.01 ± 0.17 z-

normalised, $F(1,23) = 0.37$, $p = .547$, $\eta_p^2 = .02$). We found no effect of pattern prediction on normalised hit rates (predicted = 74.25 ± 2.07%, -0.06 ± 0.16 z-normalised, surprising = 75.88 ± 2.13%, 0.06 ± 0.17 z-normalised, $F(1,23) = 3.64$, $p = .069$, $\eta_p^2 = 14$) or normalised reaction times (predicted = 388.79 ± 11.11 ms, -0.03 ± 0.18 z-normalised, surprising = 395.49 ± 11.58 ms, 0.04 ± 0.18 z-normalised, $F(1,23) = 2.46$, $p = .130$, $\eta_p^2 = .10$). There was also no interaction between prediction and feature-congruence on either normalised hit rates ($F(1,23) = 2.11$, $p = .160$, $\eta_p^2 = .08$) or normalised reaction times ($F(1,23) = 1.50$, $p = .233$, $\eta_p^2 = .06$).

The Neural Interaction Between Feature-based Attention and Prediction Replicates With a Demanding Feature-based Attention Set

We found remarkably similar neural effects in Experiment 2 (*Figures 5-7*) to those we found in Experiment 1 (*Figures 2-4*). Prediction again modulated the neural response over posterior electrodes early (standards > deviants; from 78 ms, $p < .001$) and late (standards < deviants; 246 – 348 ms, $p = .014$) in the epoch (*Figure 5B*), with opposite early (standards < deviants; 74 - 238 ms, $p < .001$) and late effects (standards > deviants; prior to 348 ms, $p < .001$) over frontal electrodes (*Figure 5A*). Follow-up comparisons revealed similar effects of prediction on each deviant type (*Figure 5C*). Over posterior electrodes, standards evoked smaller early negativities than all deviant types (orientation deviants: 109 – 160 ms, $p = .037$; colour deviants: 90 – 348 ms, $p < .001$; object deviants; 78 – 348 ms, $p < .001$) and smaller late positivities than all deviant types (orientation deviants: 227 – 348 ms, $p = .001$; colour deviants; 250 – 348 ms, $p = .029$; object deviants: 250 – 348 ms, $p = .022$). Over frontal electrodes, standards evoked smaller early positivities than all deviant types (orientation: 47 – 156 ms, $p = .0012$; colour: 98 – 242 ms, $p = .002$; object: 78 – 242 ms, $p < .001$) and smaller late negativities than orientation deviants (234 – 348 ms, $p < .001$). As in Experiment 1, we found

that the vMMN was sensitive to features of the deviant stimulus (*Figure 5C*), with object deviants evoking a significantly larger vMMN (-1.86 ± 0.27 µV) than orientation deviants (-1.10 ± 0.16 µV, $t(23) = -5.40$, $p < .001$, $BF_{10} = 288{,}942.02$) and colour deviants (-1.05 ± 0.19 µV, $t(23) = -6.17$, $p < .001$, $BF_{10} = 22{,}207{,}026.78$). Again, there was no difference between orientation and colour vMMNs ($t(23) = -0.42$, $p = .679$, $BF_{10} = 0.12$).

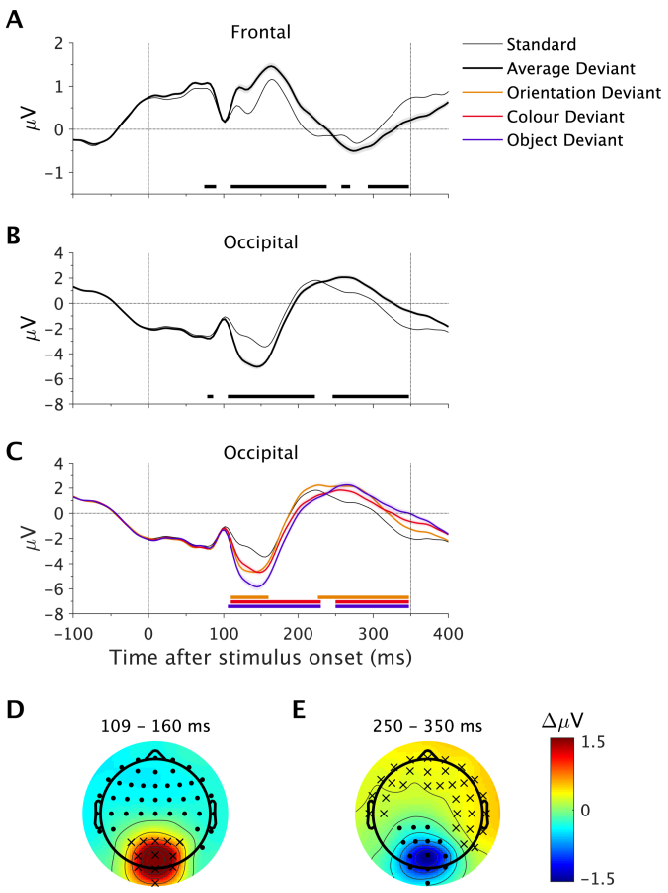

Figure 5. Main effect of prediction in Experiment 2. **(A-B)** ERPs evoked by standards and deviants (collapsed across deviant types) at frontal electrodes (Fz, F1, F3, AFz, AF3, AF4; **A**) and occipital electrodes (Oz, O1, O2, POz, PO3, PO4; **B**). Shading indicates the within-subject standard error of the mean, calculated relative to standards. Black bars along the x-axis denote significant timepoints at the displayed electrodes (cluster-corrected). (**C**) ERPs evoked by standards and each of the three deviant conditions. Shading indicates the within-subject standard error of the mean, calculated separately for each deviant condition relative to standards. Yellow, red and purple bars along the x-axis denote significant differences between standards and each corresponding deviant condition (cluster-corrected). (**D-E**) Headmaps show the effect of prediction (standard minus average deviant) during the indicated time windows. Asterisks and dots denote electrodes with larger, or smaller responses, respectively, across at least 33% of the averaged time points (cluster-corrected).

As in Experiment 1, congruent peripheral patterns evoked smaller positivities over posterior electrodes than incongruent patterns late in the epoch (195 – 273 ms, p = .045; *Figure 6B*). However, the polarity-reversed frontal effect observed in Experiment 1 did not reach significance in Experiment 2 (230 – 281 ms, p = .127).

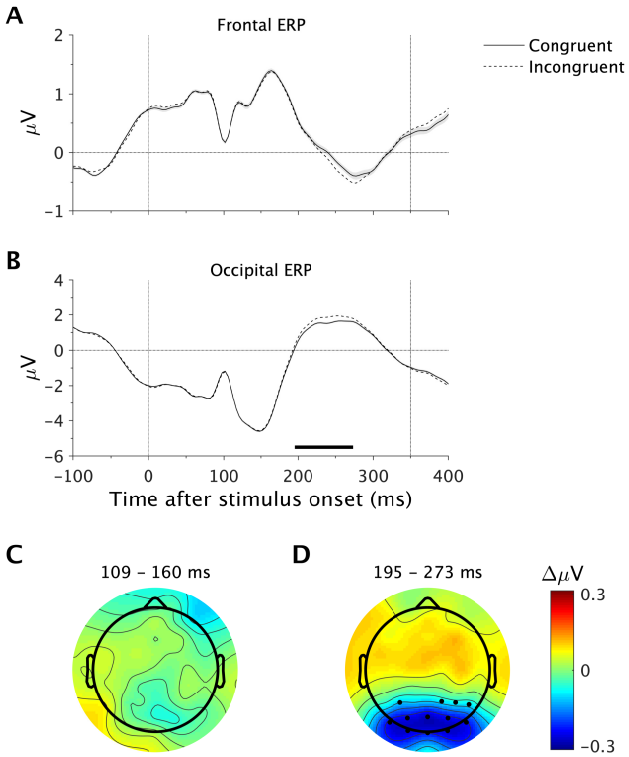

Figure 6. Main effect of feature-based attention in Experiment 2. (**A**-**B**) Congruent and incongruent ERPs are collapsed across prediction conditions separately for frontal electrodes (Fz, F1, F3, AFz, AF3, AF4; **A**) and occipital electrodes (Oz, O1, O2, POz, PO3, PO4; **B**). Shading indicates the within-subject standard error of the mean. The black bar along the x-axis denotes significant differences at the displayed electrodes (cluster-corrected). (**C**-**D**) Headmaps show the effects of feature-based attention (congruent minus incongruent) during the indicated time windows. Dots denote electrodes with smaller responses in at least 33% of the averaged time points (cluster-corrected).

Crucially, we replicated the interaction between feature-based attention and prediction that was observed in Experiment 1 (*Figure 7*). Congruent mismatch responses (deviants minus standards) were smaller than incongruent mismatch responses over posterior electrodes late in the epoch (242 – 320 ms, p = .048; *Figure 7B,H*). We also observed an additional polarity-reversed effect over frontal electrodes that was absent in Experiment 1 (254 – 324 ms, p = .026;

Figure 7A,H). Follow-up analyses revealed that feature-based attention significantly decreased the mismatch response to colour deviants (congruent = -0.01 ± 0.17 μV, incongruent = 0.31 ± 0.13 μV, $t(23) = -3.52$, $p = .002$, $BF_{10} = 94.83$, *Figure 7J*) and object deviants (congruent = 0.10 ± 0.21 μV, incongruent = 0.61 ± 0.14 μV, $t(23) = -3.66$, $p = .001$, $BF_{10} = 51.42$, *Figure 7K*) but only trended in the same direction for orientation deviants (congruent = 0.40 ± 0.11 μV, incongruent = 0.60 ± 0.10 μV, $t(23) = -1.96$, $p = .062$, $BF_{10} = 2.35$, *Figure 7I*). Again, we found no effect of feature-based attention on the vMMN evoked by any type of deviant (orientation: congruent = -1.09 ± 0.19 μV, incongruent = -1.11 ± 0.15 μV, $t(23) = .18$, $p = .857$, $BF_{10} = .12$; colour: congruent = -1.08 ± 0.19 μV, incongruent = -1.02 ± 0.22 μV, $t(23) = -0.42$, $p = .676$, $BF_{10} = .15$; object: congruent = -1.96 ± 0.28 μV, incongruent = -1.76 ± 0.27 μV, $t(23) = -1.67$, $p = .11$, $BF_{10} = 0.43$; *Figure 7C*).

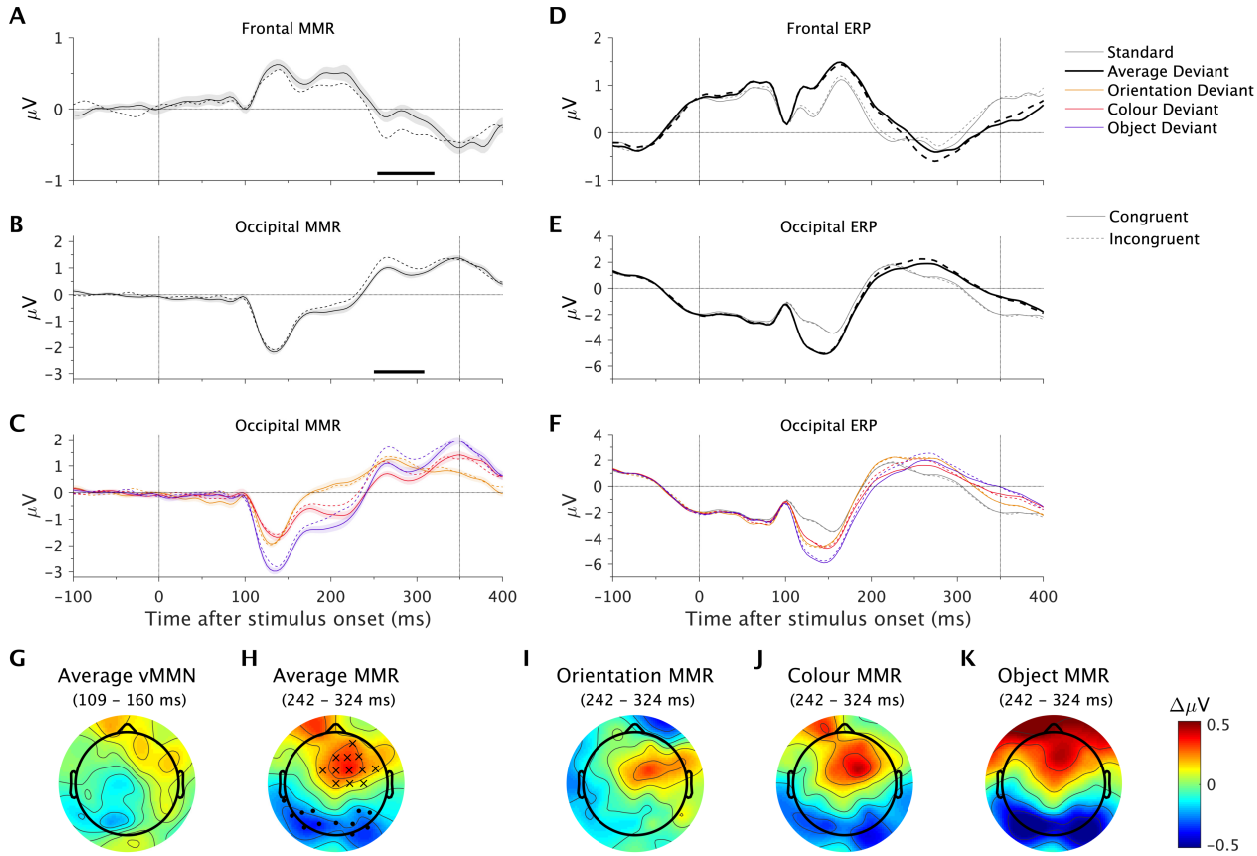

Figure 7. Interaction between feature-based attention and prediction in Experiment 2. (**A**-**B**) Average mismatch response (MMR; average deviant minus standard) collapsed across frontal electrodes (Fz, F1, F3, AFz, AF3, AF4; **A**) and occipital electrodes (Oz, O1, O2, POz, PO3, PO4; **B**). Solid lines represent the congruent condition and dotted lines represent the incongruent condition. Shading indicates the within-subject standard error of the mean. The black bar along the x-axis denotes significant differences at the displayed electrodes (cluster-corrected). (**C**) Mismatch responses at occipital electrodes for individual deviant conditions. (**D**-**E**) ERPs evoked by standards and deviants (averaged across deviant types), shown separately for congruent (solid) and incongruent (dotted) conditions. (**F**) ERPs for individual deviant conditions, shown separately for congruent (solid) and incongruent (dotted) conditions. (**G**-**H**) Headmaps show the effect of feature-based attention (congruent minus incongruent) on the average deviant mismatch response (average deviant minus standard) during the early vMMN (**G**) and late interaction time windows (**H**). Asterisks and dots denote electrodes with larger, or smaller responses, respectively, in at least 33% of the averaged time points (cluster-corrected). (**I**-**K**) Effect of feature-based attention (congruent minus incongruent) on the orientation mismatch response (**I**), colour mismatch response (**J**) and object mismatch response (**K**) during the late interaction time window. Note that cluster-based permutation tests were not conducted on these differences.

Discussion

Here we set out to investigate whether prediction interacts with feature-based attention outside the spatial focus of attention. To achieve this, we measured neural responses to surprising and predicted stimuli – deviants and standards, respectively – presented at task-irrelevant locations.

473 Task-irrelevant peripheral patterns shared features with either the targets (congruent) or
474 distractors (incongruent) in a central search task. Across two experiments, we replicated the
475 finding that feature-based attention decreased neural responses to surprising but not predicted
476 task-irrelevant stimuli in the periphery of vision. This finding suggests that the global processes
477 of feature-based attention and prediction are based on interdependent neural mechanisms, and
478 supports the theory that attention increases the gain of prediction errors (Feldman & Friston,
479 2010).

480 Consistent with previous literature, prediction modulated early and late neural responses to
481 stimuli in both experiments (*Figures 2 & 5*). Early responses (approximately 100 to 160 ms)
482 over posterior electrodes were more negative for surprising stimuli than predicted stimuli,
483 consistent with the commonly reported visual mismatch negativity (for a review, see Stefanics
484 et al., 2014). This finding is broadly consistent with the theory that top-down prediction signals
485 silence matching bottom-up sensory signals and leave only the remaining prediction error to
486 propagate forward (Friston, 2005, 2009; Rao & Ballard, 1999). Prediction also reduced the
487 later positive P3 component (from approximately 250 ms), consistent with the theory that this
488 component reflects involuntary orienting to novel stimuli (Friedman, Cycowicz, & Gaeta,
489 2001; Polich, 2007).

490 We also found that stimuli deviating in two feature dimensions (i.e., object deviants) evoked
491 larger early negativities than stimuli deviating in only one feature dimension (i.e., orientation
492 or colour deviants; *Figures 2 & 5*). This finding contradicts a previous study that found visual
493 features elicit non-additive mismatch-related brain activity (Sulykos & Czigler, 2011) and
494 suggests instead that the vMMN is sensitive to the extent of deviation across multiple feature
495 dimensions. Importantly, object deviants in Sulykos & Czigler (2011) deviated in spatial

frequency and orientation, whereas object deviants in the present study deviated in colour and orientation deviants. Thus, future studies should investigate the extent to which mismatch additivity in the visual domain depends on the specific features involved.

We found that feature-based attention reduced neural responses to task-irrelevant peripheral patterns from approximately 200 ms (*Figures 3 & 6*), consistent with the commonly reported 'selection negativity' (Gledhill et al., 2015). This effect replicated with low contrast stimuli that likely necessitated a tight focus of spatial attention (Experiment 2), contradicting the finding that feature-specific modulation of the selection negativity is contingent on spatial attention (Anllo-Vento & Hillyard, 1996; Hillyard & Münte, 1984) and suggesting instead that late effects of feature-based attention are globally effective (Gledhill et al., 2015). Interestingly, we found no difference between neural responses to congruent and incongruent stimuli earlier in the epoch (*Figures 3 & 6*), in contrast to a previous study that reported early effects of feature-based attention on neural responses to stimuli at task-irrelevant locations (beginning within 100 ms of stimulus onset; Zhang & Luck, 2009). A critical difference between Zhang & Luck (2009) and the present study is that Zhang & Luck (2009) had participants search for targets with specific feature conjunctions (luminance and colour), whereas targets in our study were defined by only a single feature (colour or orientation). Thus, it is possible that early effects of feature-based attention depend on the complexity of the attentional set. This interpretation is consistent with a recent study in which we found that neural responses to high-frequency flickering stimuli outside a search array (12.5 or 16.7 Hz, corresponding to an 80 or 60 ms cycle) are enhanced by feature-based attention during conjunction but not unique-feature search (Painter, Dux, Travis, & Mattingley, 2014).

Crucially, we found an interaction between feature-based attention and prediction in both experiments. Congruent stimuli evoked smaller posterior mismatch responses than incongruent stimuli between approximately 200 and 300 ms after stimulus onset. Inspection of the ERPs revealed that feature-based attention reduced the amplitude of neural responses to deviants but had no effect on those to standards. This pattern of results is consistent with our recent finding that attention enhances the processing of mismatch information from approximately 200 ms post-stimulus (Smout et al., 2019) and broadly supports the theory that attention enhances the gain of prediction errors (Feldman & Friston, 2010). Neural responses to surprising stimuli (deviants) are theorised to be modulated by attention because they contain prediction errors, whereas neural responses to predicted stimuli (standards) are less affected because they contain relatively few prediction errors. The present study extends this theory to suggest that feature-specific attentional modulation of prediction errors occurs even when the surprising stimuli are task-irrelevant and presented outside the spatial focus of attention.

Interestingly, we found that feature-based attention had no effect on the earlier vMMN evoked by deviants (109 – 160 ms). This pattern of findings contradicts a previous study that found the vMMN evoked by peripheral stimuli was smaller (more positive) when participants searched for a change in the deviating feature at fixation, relative to a different feature (Czigler & Sulykos, 2010). A subtle difference between the paradigms is that participants in Czigler and Sulykos (2010) searched for a feature 'change' at fixation (e.g., a change in the target object colour), whereas participants in our study searched for specific object onsets. Thus, it remains possible that subtle differences in the configuration of the attentional set can influence the timing and direction of the interaction between feature-based attention and prediction.

We manipulated target and distractor salience across the two experiments in order to investigate whether the strength of the top-down feature set modulates the interaction between prediction and feature-based attention. Although the pattern of neural effects did not differ between the two experiments, we observed slightly different behavioural effects depending on task difficulty. Responses to highly salient targets (Experiment 1) that appeared immediately after a congruent pattern were slower than those to targets that appeared after an incongruent pattern. In contrast, we observed no such effect of feature-congruence on responses to less salient targets (Experiment 2). These findings are broadly consistent with contingent capture theory (Folk, Remington, & Johnston, 1992), which proposes that distracting stimuli within the spatial focus of attention capture attention when they are congruent with the observers' current attentional set. Since targets were easily detected in Experiment 1, it seems likely that some amount of spatial attention 'leaked' to the peripheral stimuli, facilitating contingent capture. In contrast, the higher task difficulty of Experiment 2 likely necessitated a tighter focus of attention to the central stimuli, thus prohibiting a contingent capture effect.

We did not observe an effect of predictability of peripheral patterns on target detection, or an interaction between pattern prediction and feature-congruence, in either experiment. This is consistent with a previous study that failed to find any effect of pattern prediction on response times to a central feature change target, nor an interaction with task set, at the level of single trials (though note that this study did report sustained block-wise effects on behaviour; Czigler & Sulykos, 2010). In light of the neural interaction between prediction and feature-based attention observed in the present study, the lack of concurrent behavioural effects suggest that the neural bias toward congruent and surprising – but ultimately task-irrelevant – stimuli does not 'filter through' to modulate behavioural responses to task-relevant stimuli. This represents

563 an adaptive system that is not distracted by task-irrelevant events. Future research could
564 investigate whether this 'filtering' occurs during target processing or motor response stages.

565 The present study contributes to a burgeoning literature on the relationship between prediction
566 and attention. Whereas some studies have found an interaction between prediction and
567 attention (Auksztulewicz & Friston, 2015; Jiang et al., 2013; Kok, Rahnev, et al., 2012;
568 Marzecová et al., 2017; Smout et al., 2019), many others have reported only independent main
569 effects (e.g. Garrido, Rowe, Halász, & Mattingley, 2017; Hsu, Hämäläinen, & Waszak, 2014;
570 Kok, Jehee, & de Lange, 2012). We note that investigations to date have employed a wide
571 variety of attention manipulations (e.g., feature-based, spatial, temporal) and prediction
572 manipulations (e.g., first-order, rule-based) across different modalities (e.g., visual, auditory).
573 Thus, the equivocal pattern of findings to date may stem from distinct relationships between
574 different subprocesses of attention and prediction across the various modalities. In particular,
575 previous studies that found an interaction between visual attention and prediction presented
576 stimuli at attended locations (Jiang et al., 2013; Kok, Rahnev, et al., 2012; Marzecová et al.,
577 2017; Smout et al., 2019) or used paradigms that did not require focussed attention to complete
578 the task (Czigler & Sulykos, 2010), leaving open the possibility that spatial attention is
579 necessary in the interaction with prediction. Thus, the present study extends this literature by
580 demonstrating that first-order visual predictions interact with feature-based attention
581 mechanisms to modulate neural responses to stimuli outside the spatial focus of attention. The
582 nature of this interaction is consistent with the theory that attention optimises the expected
583 precision of predictions by modulating the gain of prediction errors (Feldman & Friston, 2010).
584 Future research should continue to parse 'attention' and 'prediction' into more precise
585 taxonomies that reflect specific mechanisms in the brain and investigate potential interactions

between each of these subcomponents. This work will illuminate the extent to which predictive coding theory might be considered a 'unified theory of the brain' (Friston, 2010).

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