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Evidence for spatiotemporally distinct effects of image repetition and perceptual expectations as measured by event-related potentials

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ABSTRACT

Repeated stimulus presentation leads to reductions in responses of cortical neurons, known as repetition suppression or stimulus-specific adaptation. Circuit-based models of repetition suppression provide a framework for investigating patterns of repetition effects that propagate through cortical hierarchies. To further develop such models it is critical to determine whether (and if so, when) repetition effects are modulated by factors such as expectation and attention. We investigated whether repetition effects are influenced by perceptual expectations, and whether the time courses of each effect are similar or distinct, by presenting pairs of repeated and alternating face images and orthogonally manipulating expectations regarding the likelihood of stimulus repetition. Event-related potentials (ERPs) were recorded from n = 39 healthy adults, to map the spatiotemporal progression of stimulus repetition and stimulus expectation effects, and interactions between these, using mass univariate analyses. We also tested for another expectation effect that may contribute to repetition effects in many previous experiments: that repeated stimulus identities are predictable after seeing the first stimulus in a trial, but unrepeated stimulus identities cannot be predicted. Separate blocks were presented with predictable and unpredictable alternating face identities. Multiple repetition and expectation effects were identified between 99 and 800ms from stimulus onset, which did not statistically interact at any point and exhibited distinct spatiotemporal patterns of effects. Repetition effects in blocks with predictable alternating faces were smaller than in unpredictable alternating face blocks between 117-179 ms and 506–652ms, and larger between 246 and 428ms. The distinct spatiotemporal patterns of repetition and expectation effects support separable mechanisms underlying these phenomena. However, previous studies of repetition effects, in which the repeated (but not unrepeated) stimulus was predictable, are likely to have conflated repetition and stimulus predictability effects.

Introduction

Cortical neurons adapt to dynamic and static features of an organism's environment. Repeated exposure to a stimulus often leads to reductions in responses of cortical neurons, known as repetition suppression or stimulus-specific adaptation (Desimone, 1996; Movshon and Lennie, 1979). Repetition suppression refers to a stimulus-specific reduction in a recorded signal of neuronal activity (e.g. firing rate, local field potential amplitude or fMRI BOLD signal change) to repeated compared to unrepeated stimuli (for reviews see Grill-Spector et al., 2006; Kohn, 2007; Vogels, 2016) and is one phenomenon in a wider family of adaptation effects, which includes response increases with stimulus repetition that are observed in a small range of circumstances (reviewed in Segaert et al., 2013) and exposure-dependent changes in stimulus selectivity (e.g. Sawamura et al., 2006; Wissig and Kohn, 2012). Repetition effects can also be observed in scalp-recorded event-related potentials (e.g. Schweinberger et al., 2002; Caharel et al., 2015), which are widely thought to reflect repetition suppression due to almost ubiquitous findings of suppression effects in similar experimental designs when using different recording modalities (e.g. single unit firing rate: Sawamura et al., 2006; local field potentials: De Baene and Vogels, 2010; fMRI BOLD signals: Grotheer and Kovacs, 2014, 2015).

Theories of perception based on hierarchically-organised predictive coding (Rao and Ballard, 1999; Friston, 2005) conceptualise repetition suppression as a reduction of prediction error signals due to fulfilled perceptual expectations weighted toward recently-encountered stimuli (e.g. Summerfield et al., 2008; Auksztulewicz and Friston, 2016). Repetition suppression is proposed to occur via lateral or feedback inhibition from neurons that actively generate predictions within hierarchically-organised sensory systems (Friston, 2005). This account contrasts with

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other circuit-based models which specify that reductions in stimulus-evoked responses, for example due to synaptic depression or prolonged after hyperpolarisation (Zucker and Regehr, 2002; Fioravante and Regehr, 2011; Vogels, 2016), reduce excitatory and divisive normalising inhibitory effects within local circuits (e.g. Dhruv et al., 2011; Solomon and Kohn, 2014; Kaliukhovich and Vogels, 2016). Rather than repetition suppression being driven by inhibitory connections as in predictive coding models, these models describe adaptation effects which act on lateral inhibition and can disinhibit (i.e. enhance) responses to stimuli that differ from those stimuli that have been recently seen (e.g. Patterson et al., 2013; Kaliukhovich and Vogels, 2016). Such effects can be propagated across brain areas in a feedforward manner (Kohn, 2007; Dhruv and Carandini, 2014) and are likely to interact with feedback modulatory influences, such as attention, that presumably operate on the same populations of stimulus-selective neurons (e.g. Reynolds and Heeger, 2009). It is unclear whether each class of models can account for the vast range of adaptation effects reported in the literature (reviewed in Solomon and Kohn, 2014; Whitmire and Stanley, 2016; Kaliukhovich and Vogels, 2016). However these models provide a framework for investigating repetition effects that propagate through cortical hierarchies via feedforward, feedback and lateral projections (e.g. Dhruv and Carandini, 2014; Larsson et al., 2016; Malmierca et al., 2015; Wissig and Kohn, 2012; Patterson et al., 2013).

A critical tenet of predictive coding models of repetition suppression is that magnitudes of repetition effects are modulated by the precision of sensory predictions (Auksztulewicz and Friston, 2016), and that precision can be modulated by perceptual expectations about the likelihood that a stimulus will repeat, or the likelihood that a certain stimulus will appear. Whether repetition and expectation effects are separable or interactive is unresolved (see Grotheer and Kovacs, 2016). An influential study of Summerfield et al. (2008) investigated relationships between stimulus repetition and perceptual expectations based on the likelihood that a certain stimulus (or sequence of repeating or alternating stimuli) would appear. They presented pairs of repeated and alternating faces in blocks with high and low proportions of repetition trials, and reported that BOLD repetition effects in the fusiform face area (FFA; Kanwisher et al., 1997) were larger in high repetition probability blocks. These results were interpreted as a modulation of repetition suppression by perceptual expectation, supporting precision-based predictive coding models. The findings of Summerfield et al. have been replicated several times (Kovacs et al., 2012, 2013; de Gardelle et al., 2013; Grotheer and Kovacs, 2014; Choi et al., 2017) although these expectation effects appear to be attention-dependent (Larsson and Smith, 2012) and restricted to highly familiar stimulus categories (Kovacs et al., 2013; Grotheer and Kovacs, 2014).

The repetition by block interactions in Summerfield et al. (2008) and subsequent replications may have actually identified additive effects of stimulus repetition and stimulus expectation. Responses to expected (high occurrence probability) repetitions were compared with surprising (low occurrence probability) alternations in high repetition probability blocks, and surprising repetitions with expected alternations in low probability blocks. Expected stimuli evoke smaller BOLD signals in FFA than surprising stimuli (Den Ouden et al., 2009; Egner et al., 2010), and so larger repetition effects in high repetition probability blocks are likely a result of additive effects of stimulus repetition and stimulus expectation. More recent studies (Todorovic and de Lange, 2012; Grotheer and Kovacs, 2015; Amado et al., 2016) have independently manipulated repetition and expectation by cueing different repetition probabilities using different adapter stimuli. For example, in Grotheer and Kovacs (2015) face stimuli were used as adapters and tests (i.e. the first and second stimuli presented in a trial); for a given participant female adapter faces cued a high probability of stimulus repetition within the same trial, and male adapters cued a high probability of alternation (with gender cueing assignments counterbalanced across participants). These studies have reported mixed results. Grotheer and Kovacs (2015) found additive effects that were separable in time, as originally reported by Todorovic and de Lange (2012) for ERFs following auditory stimuli at early to intermediate latencies (40–200ms) from stimulus onset. However, Amado et al. (2016) reported that repetition effects were larger for surprising stimuli, driven by large surprise-related BOLD signal increases only for alternating stimuli. This pattern is also visible in results of many earlier fMRI studies (Kovacs et al., 2012; de Gardelle et al., 2013; Larsson and Smith, 2012; Grotheer and Kovacs, 2014; Choi et al., 2017; reviewed in Kovacs and Vogels, 2014).

Our study was designed to test for electrophysiological evidence of modulations of repetition effects by perceptual expectations, and to map the spatiotemporal time courses of stimulus repetition and stimulus expectation effects using a data-driven approach. Electrophysiological evidence is especially important for evaluating predictive coding models, as prediction error signals are hypothesised to be generated by superficial pyramidal cells that contribute to scalp-recorded EEG responses (Friston and Kiebel, 2009; Auksztulewicz and Friston, 2016). It is unclear whether the larger repetition effects for surprising stimuli described above are specific to the BOLD signal, or whether they can also be identified in electrophysiological recordings. Microelectrode studies of macaque inferior temporal neurons did not report interactions between stimulus repetition and expectation for firing rates or local field potentials (Kaliukhovich and Vogels, 2011, 2014). The only ERP investigation of these effects that presented visual stimuli (Summerfield et al., 2011) used an analysis design which confounded stimulus repetition and expectation, as described above. ERP evidence (with millisecond-level temporal resolution) is also especially important for identifying separable time courses of repetition and expectation effects that may be conflated in fMRI BOLD signals.

We also investigated another type of expectation effect that may have contributed to large surprise effects for unrepeated stimuli: the difference in stimulus identity predictability across repeated and alternating stimulus conditions. In the experiments described above adapter and test stimuli (i.e. the first and second stimuli presented in each trial) were the same stimulus image in repetition trials. In these trials the image properties of the repeated stimulus could be predicted after viewing the adapter stimulus. However, each alternating test stimulus was randomly-chosen from a large stimulus set, and so image-specific expectations could not be formed for alternating test stimuli (i.e. the alternating stimuli were unpredictable). Surprise-related signal increases for alternating stimuli may have arisen from violations of image-specific expectations of repeated stimuli. However, no image-specific expectations regarding alternating stimuli could be formed or violated, preventing large signal increases for surprising repetitions. Additionally, it is possible that repetition effects observed in these widely-used stimulus repetition designs are caused or enhanced by imbalances of stimulus expectations available for repeated and alternating stimuli (Feuerriegel, 2016; Pajani et al., 2017).

We investigated relationships between stimulus repetition effects and perceptual expectations by presenting repeated and alternating face pairs in high and low repetition probability contexts (expected and surprising repetitions and alternations), and conditions in which neither the repeated or alternating stimulus was preferentially expected (neutral stimuli, corresponding to the ‘unpredicted’ stimulus condition in Arnal and Giraud, 2012). Our orthogonal manipulation of stimulus repetition and stimulus expectation allowed us to separately assess repetition effects for expected, neutral and surprising stimuli, which has not been done in electrophysiological studies using visual stimuli. In addition, we presented separate experimental blocks in which alternating face stimuli were either predictable or unpredictable, allowing us to investigate predictability effects and how they may contribute to observed repetition effects. Using mass univariate analyses of ERPs we were able to map the spatiotemporal patterns of repetition, expectation and predictability effects following stimulus onset. We aimed to identify latencies from stimulus onset at which repetition effects are modulated by perceptual expectations, or by the ability to predict the alternating stimulus image. By using a data-driven analysis approach we could also assess whether repetition and expectation effects exhibited similar or distinct spatiotemporal patterns, and by extension whether such effects are likely to share similar neural substrates. By allowing image-specific expectations for alternating faces we were also able to test whether the large surprise-related responses for alternating stimuli (e.g. Amado et al., 2016) could be found for repeated stimuli (i.e. when image-specific expectations for alternating stimuli are violated). We expected to find larger ERP repetition effects for surprising stimuli, consistent with existing fMRI evidence (e.g. Amado et al., 2016; de Gardelle et al., 2013), and larger ERP repetition effects in experimental blocks with unpredictable alternating faces.

Methods

Participants

Thirty-nine people participated in this experiment (10 males, mean age 25.3 ± 5.5, age range 18–38). All participants were native English speakers and had normal or corrected-to-normal vision, and were right-handed as assessed by the Flinders Handedness Survey (Nicholls et al., 2013). Three participants were excluded from analyses due to excessively noisy data. This experiment was approved by the Human Research Ethics committee of the University of South Australia.

Stimuli

Examples of stimuli are shown in Fig. 1A. Ninety frontal images of faces (45 male, 45 female, neutral expression) were taken from the NimStim face database (Tottenham et al., 2009) and the Minear and Park Ebner face set (Minear and Park, 2004; Ebner, 2008). Images were converted to greyscale and cropped, resized and aligned so that the nose was in the horizontal center of the image and eyes of each face were vertically aligned. Image backgrounds were equated across Minear and Park and NimStim faces. Images were resized so that at a viewing distance of

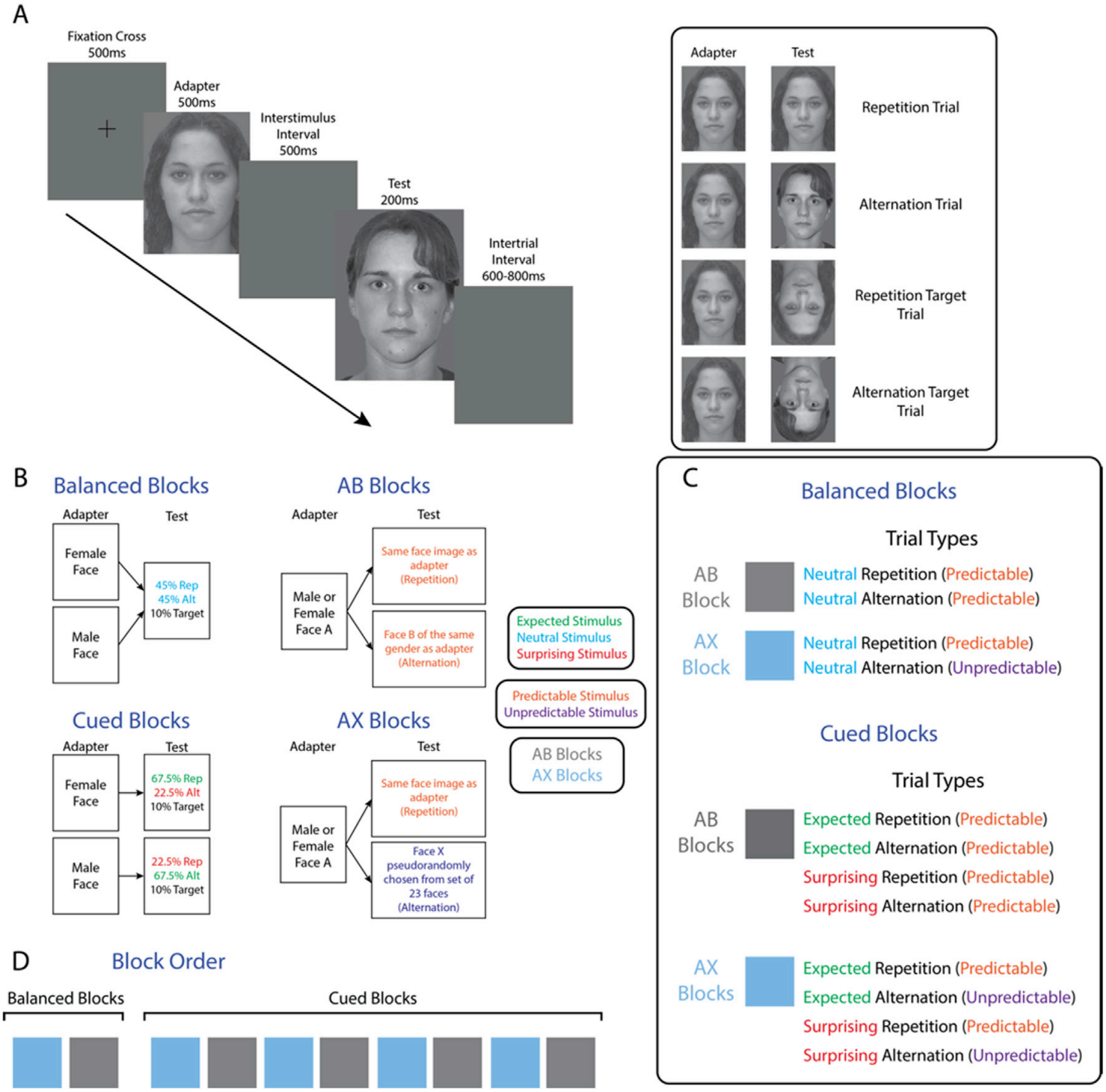

Fig. 1. Trial diagram and repetition probability cueing design. A) In each trial adapter and test stimuli were presented separated by a 500 ms interstimulus interval. Test stimuli were 20% larger than adapters. Examples of stimuli in each trial type are shown on the right. B) Examples of experimental block types. In balanced blocks the probability of stimulus repetition is 45%. In cued blocks the probability of stimulus repetition varied by the gender of the adapter face. In this example a female adapter cues a high (67.5%) probability of stimulus repetition, whereas a male adapter cues a low (22.5%) probability of stimulus repetition. In AB blocks the test face could either be the same image as the adapter (repetitions), or a different specific face of the same gender (alternations). In AX blocks the test face could be the same image as the adapter (repetitions) or a face of the same gender as the adapter, pseudorandomly-chosen from a set of 23 faces (alternations). C) Trial types within each block type. Trials are colour-coded according to whether they are expected/neutral/surprising and whether the test face identity is predictable/unpredictable. D) Block order in the experiment. Balanced blocks were always presented before cued blocks. AB and AX blocks alternated and this order was counterbalanced across participants. (two-column fitting image).

60 cm stimuli subtended approximately 3.15° × 4.30° of visual angle (135 × 180 pixels). Test stimulus images were created 20% larger than adapters. The SHINE toolbox (Willenbockel et al., 2010) was used to equate mean pixel intensity and contrast across images (Mean normalised pixel intensity = 0.38, mean RMS contrast = 0.12). Stimuli were presented against a grey background (normalised pixel intensity = 0.44).

Procedure

Participants sat in a well-lit testing room 60 cm in front of an LED monitor (refresh rate 60 Hz). Stimuli were presented using custom scripts written in MATLAB (Mathworks) using functions from PsychToolbox v3.0.11 (Brainard, 1997; Kleiner et al., 2007). Behavioural responses were recorded using a one-button response box connected to the EEG amplifier.

In each trial face stimuli were presented as adapters (500 ms) and tests (200 ms) separated by a 500 ms interstimulus interval (ISI) as shown in Fig. 1A. Adapter faces were preceded by a fixation cross for 500 ms. The intertrial interval (including fixation cross presentation duration) varied pseudorandomly between 1100 and 1300ms. Adapter and test stimuli were either the same face image (repetition trial) or two different faces of the same gender (alternation trials).

In target trials the test face was inverted along the horizontal plane (as done by Summerfield et al., 2008), and could be a repeated or alternating face with equal probability. Upon seeing a target participants were instructed to press a button on the response box as quickly as possible (response hands counterbalanced across participants). Responses between 200 and 1000ms from test stimulus onset were counted as correct responses. Target trials were presented as 10% of all trials.

There were 10 experimental blocks: 2 balanced blocks and 8 cued blocks (Fig. 1B). Trial types within each block are shown in Fig. 1C, and experimental block order is shown in Fig. 1D. Balanced blocks were always presented before cued blocks to avoid carry-over effects of expectations from cued blocks. These blocks included trials with different stimulus repetition and alternation probabilities, which could be implicitly learned with exposure to multiple trials to form expectations about the likelihood of seeing repeated and alternating face images (as done by Summerfield et al., 2008, 2011). In balanced blocks there were equal numbers of repetition and alternation trials (45% each). Trials in these blocks are termed neutral repetitions and neutral alternations (corresponding to unpredicted conditions in the framework of Arnal and Giraud, 2012), as participants should not learn to preferentially expect any particular test stimulus in these blocks. The remaining 10% were target trials (5% repeated face targets, 5% alternating face targets). In cued blocks the probability of repetition was determined by the adapter face gender (overall probability of repetition 45%). As an example, for one participant female adapter faces signalled a high (67.5%) probability of stimulus repetition (expected repetitions) and a low (22.5%) probability of an alternation (surprising alternations). For the same participant male adapters signalled a low probability of repetition (surprising repetitions) and a high probability of an alternating trial (expected alternations). Participants could form expectations during the cued blocks based on implicit learning of statistical associations between the adapter face gender and the probability of stimulus repetition or alternation within a trial (as done by Grotheer and Kovacs, 2015), and so high probability stimuli are termed expected repetitions/alternations and low probability stimuli are termed surprising repetitions/alternations. Gender cueing assignments were counterbalanced across participants.

Balanced and cued blocks were further subdivided into two block types, which differed with respect to the alternating test face identities (Fig. 1B). In both block types 4 faces (2 male, 2 female) were presented as adapters and repeated test stimuli (different faces used in each block). In repetition trials one of these faces appeared as both the adapter and test, with the restriction that the adapter in one trial could never be the test face in the preceding trial. In the first block type (AB blocks) alternating test faces were the other face identity of the same gender as the adapter. For example, if female face A was presented as the adapter then the test face could either be a repeat (AA) or the other female face (AB). In AB blocks participants could learn through repeated adapter-test face pairings to expect either the same face as the adapter stimulus (Face A) in repetition trials, or another specific face identity (Face B) in alternation trials, and so the alternating test faces were predictable in these blocks. In these blocks expectations could therefore be formed for both specific face images and repetition/alternation trial types. In the second block type (AX blocks) the alternating face image was chosen randomly from a separate set of 46 faces (23 male, 23 female), with the restriction that each of the 23 faces within a gender set must be presented once before any face identity could be shown again. Adapters and tests were of the same gender in each trial. For example, if female face A was presented as the adapter, the test face could either be a repeat (AA) or a different randomly-selected female face (AX). In these blocks participants could not learn to expect any specific face identity for alternating trials, and so the alternating test stimuli were unpredictable. In these blocks expectations could be formed regarding the likelihood of repetition/alternation trials, however face image-specific expectations could only be formed for repeated stimuli. These AB and AX trials were presented within separate blocks to minimise the need for learning face image-specific AB alternating stimulus associations prior to the experiment. AB and AX blocks alternated throughout the experiment. There was one AB block and one AX block in the set of 2 balanced blocks, and 4 AB and 4 AX blocks within the 8 cued blocks. The order of AB and AX blocks (which occurred first) was counterbalanced across participants. Face images used for adapter and repeated test stimuli allocated to each block were also counterbalanced across participants. A practice block was also presented before the experiment (AB block, 24 trials, using a separate set of 4 faces).

A total of 1780 trials (1600 nontarget trials and 180 target trials) were presented. In balanced blocks there were 80 nontarget trials for each neutral repeated and alternating condition. In cued blocks there were 240 nontarget trials for each expected repetition and expected alternation condition, and 80 nontarget trials for each surprising repetition and surprising alternation condition. Target trials were allocated in proportion to the number of nontarget trials in each condition (24 target trials each for expected repetition and alternation conditions, and 8 target trials each for surprising/neutral repetition and alternation conditions). Balanced blocks contained 178 trials each and lasted approximately 7.1 min each. Cued blocks contained between 177 and 179 trials and lasted approximately 7.2 min each. Ten blocks were included within the experiment to present at least 80 trials per nontarget condition, in order to derive high signal-to-noise ratio estimates of ERPs for each participant. Total testing time (excluding breaks) was 71.4 min.

EEG recording and data processing

EEG was recorded from 128 active electrodes using a Biosemi Active Two system (Biosemi, the Netherlands). Recordings were grounded using common mode sense and driven right leg electrodes (http://www.biosemi.com/faq/cms&drl.htm). Eight channels were added: two electrodes placed 1 cm from the outer canthi of each eye, four electrodes placed above and below each eye, and two electrodes placed on the left and right mastoids. EEG was recorded at 1024 Hz (DC-coupled with an anti-aliasing filter, -3 dB at 204 Hz). Electrode offsets were kept within ±50 µV.

EEG data were processed using EEGLab V.13.4.4b (Delorme and Makeig, 2004) and ERPLab V.4.0.3.1 (Lopez-Calderon and Luck, 2014) running in MATLAB (The Mathworks). EEG data were downsampled to 512 Hz offline. A photosensor was used to measure the timing delay of the video system (10 ms) and stimulus event codes were shifted offline to account for this delay. 50 Hz line noise was identified using Cleanline (Mullen, 2012) using a separate 1 Hz high-pass filtered dataset (EEGLab Basic FIR Filter New, zero-phase, finite impulse response, -6 dB cutoff frequency 0.5 Hz, transition bandwidth 1 Hz). Identified line noise was subtracted from the unfiltered dataset (as recommended by

Bigdely-Shamlo et al., 2015). Excessively noisy channels were identified by visual inspection (mean noisy channels by participant = 1.4, median 1, range 0–4) and were excluded from average referencing and independent components analysis (ICA). Data was then referenced to the average of the 128 scalp channels. One channel (FCz) was removed to correct for the rank deficiency caused by average referencing. A separate dataset was processed in the same way, except a 1 Hz high-pass filter was applied (filter settings as above) to improve stationarity for the ICA. ICA was performed on the 1 Hz high-pass filtered dataset (RunICA extended algorithm, Jung et al., 2000). Independent component information was transferred to the unfiltered dataset. Independent components associated with ocular and muscle activity were identified and removed according to guidelines in Chaumon et al. (2015). Noisy channels and FCz were then interpolated from the cleaned data (spherical spline interpolation). EEG data were low-pass filtered at 30 Hz (EEGLab Basic Finite Impulse Response Filter New, zero-phase, -6 dB cutoff frequency 33.75 Hz, transition band width 7.5 Hz). Data were epoched from −100ms to 800 ms from test stimulus onset and baseline-corrected using the prestimulus interval. Epochs containing ±100 μV deviations from baseline and nontarget trials containing button press responses were rejected.

Statistical analyses

ERPs were analysed at each electrode and time point using mass univariate repeated measures ANOVAs implemented in the LIMO EEG toolbox v1.4 (Pernet et al., 2011). All time points between −100 and 800 ms at all 128 scalp electrodes were included in each analysis (59,008 comparisons). Corrections for multiple comparisons were performed using spatiotemporal cluster corrections based on the cluster mass statistic (Bullmore et al., 1999; Maris and Oostenveld, 2007). 2 × 3 × 2 repeated measures ANOVAs with the factors block (AB/AX), expectation (expected/neutral/surprise) and repetition (repeated/alternating) were performed using the original data and 1000 bootstrap samples. For analyses of main effects and two-way interactions ERP data were averaged across levels of factors not of relevance to that main effect or interaction. For example, data were averaged over AB and AX blocks and expected/neutral/surprising conditions when analysing main effects of repetition, and averaged over AB/AX blocks when analysing repetition by expectation interactions. Similarly, data were averaged over expectation conditions for analyses of the block by repetition interactions. Data were averaged across trials within each condition, and then across conditions. For each bootstrap sample data from all conditions were mean-centred, pooled and then sampled with replacement and randomly allocated to each condition (bootstrap-t method). For each bootstrap sample, all F ratios corresponding to uncorrected p-values of <0.05 were formed into clusters with any neighbouring such F ratios. Channels considered spatial neighbours were defined using the 128-channel Biosemi channel neighbourhood matrix in the LIMO EEG toolbox (Pernet et al., 2011, 2015). Adjacent time points were considered temporal neighbours. The sum of the F ratios in each cluster is the ‘mass’ of that cluster. The largest cluster masses in each of the 1000 bootstrap samples were used to estimate the distribution of the null hypothesis. Cluster masses of each cluster identified in the original dataset were compared to the null distribution; the percentile ranking of each cluster relative to the null distribution was used to derive its p-value. The p-value of each cluster was assigned to all members of that cluster. Channel/timepoint combinations not included in any statistically significant cluster were assigned a p-value of 1. These cluster-based multiple comparisons corrections were used because they provide control over the weak family-wise error rate while maintaining high sensitivity to detect broadly-distributed effects (Maris and Oostenveld, 2007; Groppe et al., 2011).

To isolate repetition probability expectation effects signalled by adapter faces in cued blocks, 2 × 2 × 2 repeated measures ANOVAs without neutral conditions were performed with cluster-based corrections as described above.

Results

Task performance

Accuracy for detecting and responding to targets collapsed across conditions was high (mean accuracy 97%, range 77–100%). Mean reaction time collapsed across conditions was 470 ± 60 ms (range 358–654ms). Accuracy and reaction times were not compared across conditions. This was because of the low number of targets allocated to each condition, and that the task was designed to maintain attention towards nontarget stimuli.

Mass univariate analyses of ERPs

Main effects of repetition

Mass univariate analyses comparing repeated and alternating stimuli (averaged across AB/AX and expectation conditions) revealed repetition effects spanning 99–800ms from test stimulus onset (displayed in Fig. 2A). Grand average ERP waveforms evoked by repeated and alternating stimuli at example electrodes are displayed in Fig. 2B.

Repetition effects could be broadly divided into 6 time windows (shown in Fig. 2C). During the first time window (99–168ms) repeated stimuli evoked more negative-going waveforms at posterior electrodes and more positive waveforms at frontal channels. During the second time window (170–209ms) repeated stimuli evoked more negative-going waveforms at right parietal electrodes. During the third time window (211–359ms) repeated stimuli evoked more negative-going waveforms over bilateral occipitotemporal sites, and more positive-going waveforms over frontocentral channels. During the fourth time window (375–537ms) repeated stimuli evoked more negative-going waveforms at posterior channels, and more positive-going waveforms at frontal and frontocentral channels. During the fifth time window (539–685ms) ERPs were more negative to repeated stimuli at right occipiotemporal channels, and more positive at central and left frontal channels. During the sixth time window (720–800ms) repeated stimuli evoked more positive-going waveforms over bilateral posterior electrodes.

Main effects of expectation

Comparisons of expected, neutral and surprising stimuli (averaged across repeated/alternating and AB/AX conditions) revealed main effects of expectation at time points spanning 113–703ms from test stimulus onset (Fig. 3A). Importantly, these only partially overlapped in time with main effects of repetition and showed distinct spatiotemporal patterns of effects (Fig. 3B). Grand average ERPs to expected, neutral and surprising stimuli at example electrodes are displayed in Fig. 3D. Expectation effects could be broadly split into 5 distinct time windows (displayed in Fig. 3D). There was an early (113–144ms) over frontal electrodes, followed by an effect between 152 and 263ms over bilateral occipital, central and frontal electrodes, a third cluster (275–340ms) at central channels, a fourth cluster (342–433ms) at bilateral occipital, central and right frontocentral channels, and a late (435–703ms) effect over right frontocentral and left occipital electrodes.

As there were large differences between ERPs evoked by neutral compared to both expected and surprising stimuli, we ran additional analyses to investigate whether these differences were due to block order effects (as neutral stimuli in balanced blocks were always presented before expected/surprising stimuli in cued blocks). To do this, ERPs evoked by adapter stimuli from balanced and cued blocks (pooled across repetition, expectation and AB/AX block conditions) were compared using mass univariate one-way ANOVAs (factor levels balanced block vs. cued block), as such differences in adapter stimulus-evoked ERPs would include any block order effects. There was substantial overlap between expectation and block order effects between 162 and 273ms (Fig. 3C), indicating that effects during this period were likely due to block order. Expectation and block order effects partially overlapped across electrode/timepoint combinations in other time windows.

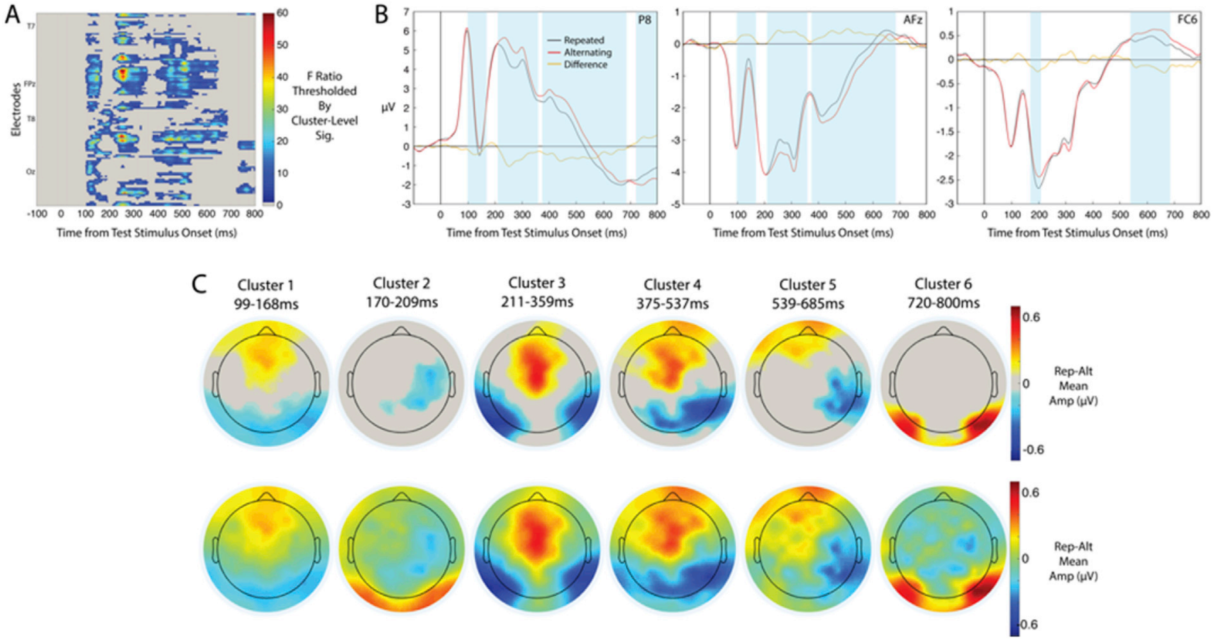

Fig. 2. Results of mass univariate repetition effect analyses. A) Timepoint-by-channel matrix of repetition effects. F ratios are displayed thresholded by cluster-level statistical significance (F ratios ≤0.94 also changed to grey). B) Grand-average ERPs evoked by repeated and alternating stimuli. Shaded areas correspond to time windows of repetition effects defined in Fig. 2B, for electrodes showing significant effects within each time window. C) Scalp maps of repetition effects by latency from test stimulus onset. Each scalp map shows the mean [repetition - alternation] amplitude difference over the time window, for channel/timepoint combinations included in statistically significant clusters (top row) and all channels (bottom row). (two-column fitting image).

Repeated measures ANOVAs excluding neutral conditions identified 2 clusters of expectation effects (shown in Fig. 3D). During the first cluster (117–144ms) expected stimuli evoked more positive-going waveforms at left frontal channels. During the second cluster of effects (328–375ms) ERPs were more negative to expected stimuli over bilateral frontal electrodes.

Interactions involving expectation and repetition

ERP repetition effects for expected, neutral and surprising stimuli (averaged over AB and AX block types) are displayed at example channel P8 in Fig. 3F and were highly similar across the epoch. There were no significant clusters of expectation by repetition interactions, or block by expectation by repetition interactions.

As noted by a reviewer, expectation effects are likely to build up over trials as participants gradually learn stimulus repetition/alternation probabilities during the cued blocks. As a result, by averaging over all cued blocks the expectation effects (and repetition-by-expectation interactions) may have been underestimated for this experiment. To test for changes in expectation effects over the course of the cued blocks we calculated the cluster mean amplitudes across electrode/timepoint combinations within expectation effect clusters 1 and 2 (from analyses without neutral conditions) for each nontarget trial in the cued blocks. The 20% trimmed mean was used to derive cluster mean amplitudes, to reduce effects of asymmetries or outliers when averaging over cluster-defined ROIs (see Friston et al., 2006). Within-subject regressions were performed on cluster mean amplitudes with the predictor of trial number across all cued blocks (ranging from 1 to 1424) for expected and surprising stimuli separately. Beta estimates were then compared across expected and surprising stimuli for each cluster (as done by Todorovic and de Lange, 2012) using Yuen's paired-samples t tests based on the 20% trimmed mean (Yuen, 1974) which is a robust alternative to Student's t. Differences in beta values for expected and surprising stimuli indicate that the size of the expectation effect linearly changed throughout the cued blocks. Expectation effects across cued blocks are displayed in Fig. 4. There were no statistically significant differences in beta values across expected and surprising conditions, for expectation effect cluster 1 ($t(21) = -0.30$, $p = .767$) or cluster 2 ($t(21) = 0.66$, $p = .51$) indicating that the size of expectation effects remained relatively stable throughout the cued blocks.

Predictability x repetition interactions

There were 3 significant repetition by block interaction clusters between 117 and 652ms (Fig. 5A) which partly overlapped with main effects of repetition (Fig. 5B). Topographies of significant interaction clusters are displayed in Fig. 5C. Grand-average ERPs evoked by repeated and alternating stimuli in each block type, averaged across expectation conditions, at example channel P8 are shown in Fig. 5D. During the first significant interaction cluster (117–179ms) repetition effects were larger in AX compared to AB blocks over bilateral posterior and frontal channels. During the second cluster (246–428ms) the opposite pattern was observed, with larger repetition effects in AB compared to AX blocks. During the third cluster (506–652ms) repetition effects were larger in AX blocks over right occipitotemporal and left frontocentral channels. These interactions were driven by AB/AX block differences for alternating stimulus-evoked ERPs, with no visible block effects on responses to repeated stimuli.

Additional comparisons were performed across adapter stimuli from AB and AX blocks, using mass-univariate analysis methods as described above, to ascertain whether block differences were specific to test stimuli. There was a single significant cluster spanning 414–506ms over right posterior channels, during which ERPs evoked by adapters in AB blocks were more negative than those in AX blocks (Fig. 5E). However this effect showed minimal overlap with the repetition by block interaction effects for test stimuli (Fig. 5F).

Discussion

The major finding from this study is that stimulus repetition and stimulus expectation effects, as measured by ERPs, exhibited different spatiotemporal patterns relative to stimulus onset, indicating distinct neural mechanisms underlying each effect. Furthermore, we did not find any evidence that repetition effects were modulated by perceptual

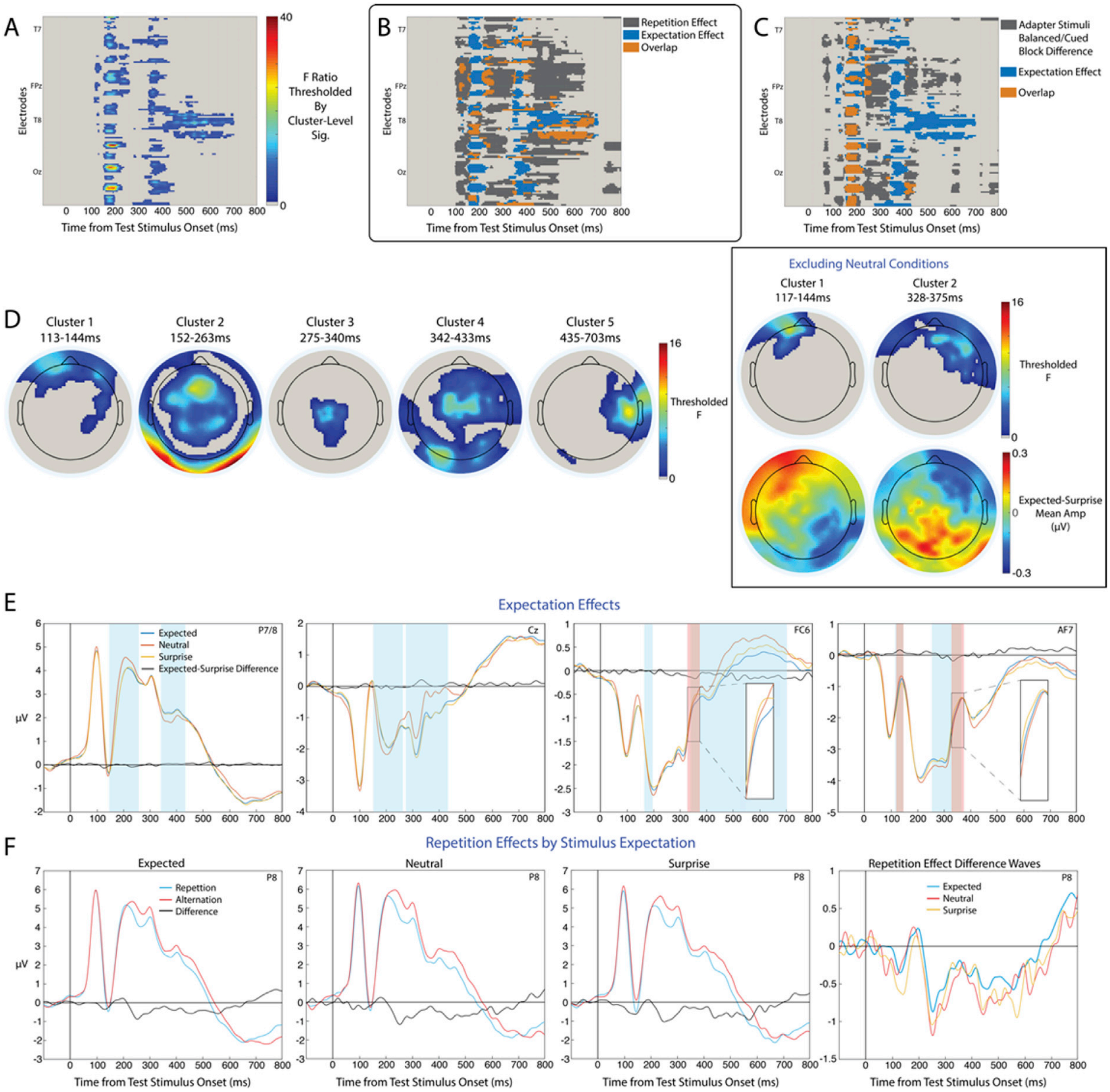

Fig. 3. Results of mass univariate expectation effect analyses. A) Timepoint-by-channel matrix of expectation effects. F ratios are thresholded by cluster-level statistical significance (F ratios ≤0.63 also changed to grey). B) Timepoint-by-channel matrix of the spatiotemporal overlap of repetition and expectation effects. C) Timepoint-by-channel matrix of the spatiotemporal overlap of expectation effects and differences in adapter-evoked responses across balanced and cued blocks (block order effects). D) Scalp maps of expectation effects by latency from test stimulus onset. Average F ratios across each time window are displayed for electrodes within statistically significant clusters (F ratios ≤0.25 changed to grey). Results of analyses excluding neutral conditions are shown in the boxed area, with [expected – surprising] ERP mean amplitude differences shown under F ratios for each cluster. E) Grand-average ERPs evoked by expected, neutral and surprising test stimuli at selected channels. Shaded areas correspond to time windows of expectation effects defined in Fig. 3C, for electrodes showing significant effects within each time window (blue = analyses including neutral conditions, red = analyses excluding neutral conditions). F) Grand-average ERPs showing stimulus repetition effects for expected, neutral and surprising stimuli. (two-column fitting image).

expectations. We identified a complex progression of stimulus repetition and stimulus expectation effects from 99 ms post stimulus onset until the end of the 800 ms epoch. Stimulus repetition and expectation effects did partially overlap in time and across electrodes, but did not statistically interact. However, there were differences in the magnitude of repetition effects across blocks of predictable and unpredictable alternating face stimuli. These block differences indicate that repetition effects observed in many previous studies, which presented predictable repeated faces and unpredictable alternating faces, may have conflated effects of repetition and stimulus predictability.

Stimulus repetition effects

A range of ERP face image repetition effects could be identified spanning 99–800ms from stimulus onset (displayed in Fig. 2) including novel and previously reported effects (reviewed in Schweinberger and Neumann, 2016). An early repetition effect spanned 99–168ms and was similar to previously observed face image repetition effects (e.g. Herzmann et al., 2004; Jemel et al., 2005; but see Caharel et al., 2015). This repetition effect appears to be a more negative-going waveform during the visual P1 component, with the effect extending into the time window of the N170 (discussed in Rossion and Jacques, 2007). This effect and a later repetition effect spanning 170–209ms from stimulus onset may be due to repetition of low- or mid-level image properties, for example stimulus shape. As we presented repetitions of low-level visual information in addition to facial identity information, these early repetition effects should be interpreted as image repetition rather than face identity repetition effects. We also identified the N250r face repetition effect

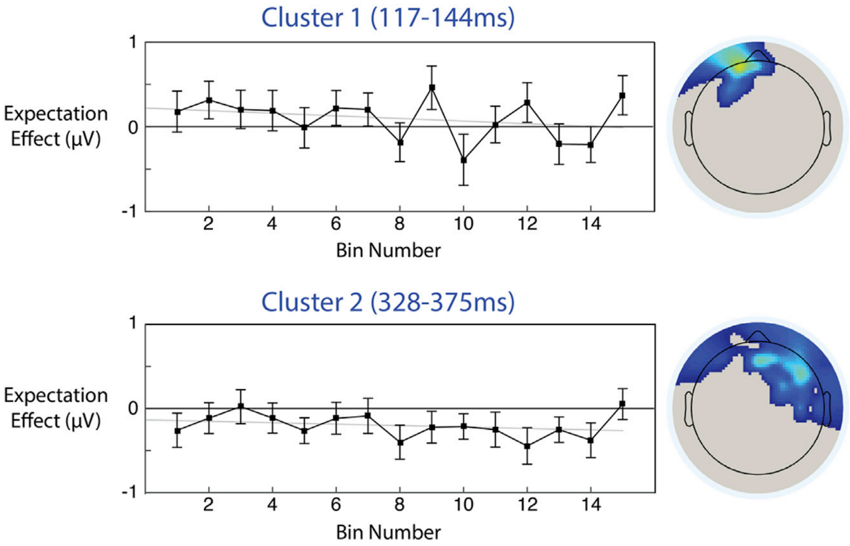

Fig. 4. Expectation effects in cued blocks over the course of the experiment. Differences in cluster mean amplitudes between expected and surprising stimuli (pooled over repetition/alternation and AB/AX conditions) are displayed for each cued expectation effect cluster identified in analyses that excluded neutral conditions. Expected and surprising trials were ordered by trial number within the cued blocks sorted into 15 bins each, with equal numbers of trials across bins for a condition (approx. 60 trials per participant per bin for expected conditions, 20 trials per bin for surprising trials). Expected-Surprising differences in mean amplitudes (averaged across trials within the same bin) are displayed for each bin. Error bars represent standard errors of the mean. Grey lines represent linear regression lines fit to the bin-averaged difference scores. (one-column fitting image).

(Schweinberger et al., 2002) spanning 211–359ms from stimulus onset. This effect is larger for face image repetitions (as in our study) compared to when presenting different images of the same face identity (Schweinberger et al., 2002; Caharel et al., 2015; Schweinberger and Neumann, 2016) suggesting that the N250r effect in our data reflects both local and feedforward-inherited effects, characteristic of image repetition effects in high-level visual areas (Vogels, 2016).

Later repetition effects between 375 and 537ms from stimulus onset differed in direction and topography to previously reported face repetition or semantic/categorical priming effects at similar latencies (e.g. Schweinberger et al., 2002; Wiese and Schweinberger, 2015). These repetition effects may index influences on local recurrent network activity, as found in macaque inferior temporal neurons (Kaliukhovich and Vogels, 2016) and in V1 (Patterson et al., 2013). However, these effects may also index recurrent feedforward and feedback interactions across high-level visual regions (e.g. Ewbank et al., 2011). The late repetition effect from 720 to 800ms (until the end of the analysed epoch) appears too late to reflect purely local recurrent network activity as reported in Kaliukhovich and Vogels (2016) and may reflect modulation of activity by higher level visual areas, as found in the auditory system (Malmierca et al., 2015).

It is likely that these early and late ERP effects with similar topographies index qualitatively different repetition effects, which may also be associated with distinct changes in stimulus selectivity (e.g. Patterson et al., 2013; Kaliukhovich and Vogels, 2016). This would imply that BOLD repetition effects index a mixture of these early and late repetition effects, which may also be conflated in studies of directed connectivity modulations by stimulus repetition (e.g. de Gardelle et al., 2013; Choi et al., 2017).

Stimulus expectation effects

Multiple expectation effects were found spanning 113–703ms from stimulus onset (shown in Fig. 3). Contrary to our expectations there were several time periods in which ERPs to neutral stimuli were markedly different to both expected and surprising stimuli. Effects spanning approximately 152–263ms are likely due to block order effects, as similar patterns were found when comparing adapter stimulus-evoked responses across balanced and cued blocks. Block order effects could not be separated in our design, as balanced blocks containing neutral stimuli were always presented before cued blocks containing expected and surprising stimuli. However other experiments controlling for the confound of time have reported smaller BOLD responses to neutral compared with both expected and surprising stimuli (Rahnev et al., 2011; Amado et al., 2016). This suggests that expectation effects, operationalised as stimulus appearance probability, may include different contributions of expectation fulfilment, surprise, and the ability to form expectations for upcoming stimuli (Kovacs and Vogels, 2014; Hsu et al., 2015; Grotheer and Kovacs, 2016). Such effects should be further investigated using designs that control for block order (for example Amado et al., 2016).

Analyses were performed excluding neutral blocks in order to isolate effects of stimulus expectations that were cued by adapter stimuli. These analyses revealed an early expectation effect from 117 to 144ms and a later effect from 328 to 375ms from stimulus onset. The early effect was statistically significant at frontal channels, however the topography of this effect (shown in Fig. 3D) suggests sources in extrastriate visual cortex. This is because there was increased negativity for expected stimuli at electrodes over right extrastriate cortex, and a more spatially-distributed opposite-dipole effect at left frontal channels (which would be more likely detected using our cluster-corrected analyses, discussed in Groppe et al., 2011). This effect topography is consistent with expectation effects based on stimulus transition probabilities in inferior temporal neurons, developed through repeated pairing of stimulus images within trials (Turk-Browne et al., 2009; Meyer and Olson, 2011; Meyer et al., 2014a; Ramachandran et al., 2016; Kaposvari et al., 2016). This early effect may be related to similar early (100–200ms) effects of expectations based on repeatedly-paired stimuli in audition (Todorovic and de Lange, 2012). However, as there were not statistically-significant effects at posterior electrodes, the sources of such effects remain speculative and should be verified in future experiments.

The later (328–375ms) expectation effect was consistent with frontally-generated effects found when manipulating expectations for abstract stimulus sequences (e.g. expectations of repeated stimulus pairs) that are not associated with any specific stimulus images (e.g. Summerfield et al., 2011). This late effect may correspond to BOLD expectation effects in inferior frontal and middle frontal gyri (Grotheer and Kovacs, 2015; Amado et al., 2016; Choi et al., 2017) and dorsolateral prefrontal cortex (Den Ouden et al., 2009; Rahnev et al., 2011). Importantly, these expectation effects are distinct from expectations based on stimulus transition probabilities, and are not found at earlier latencies in

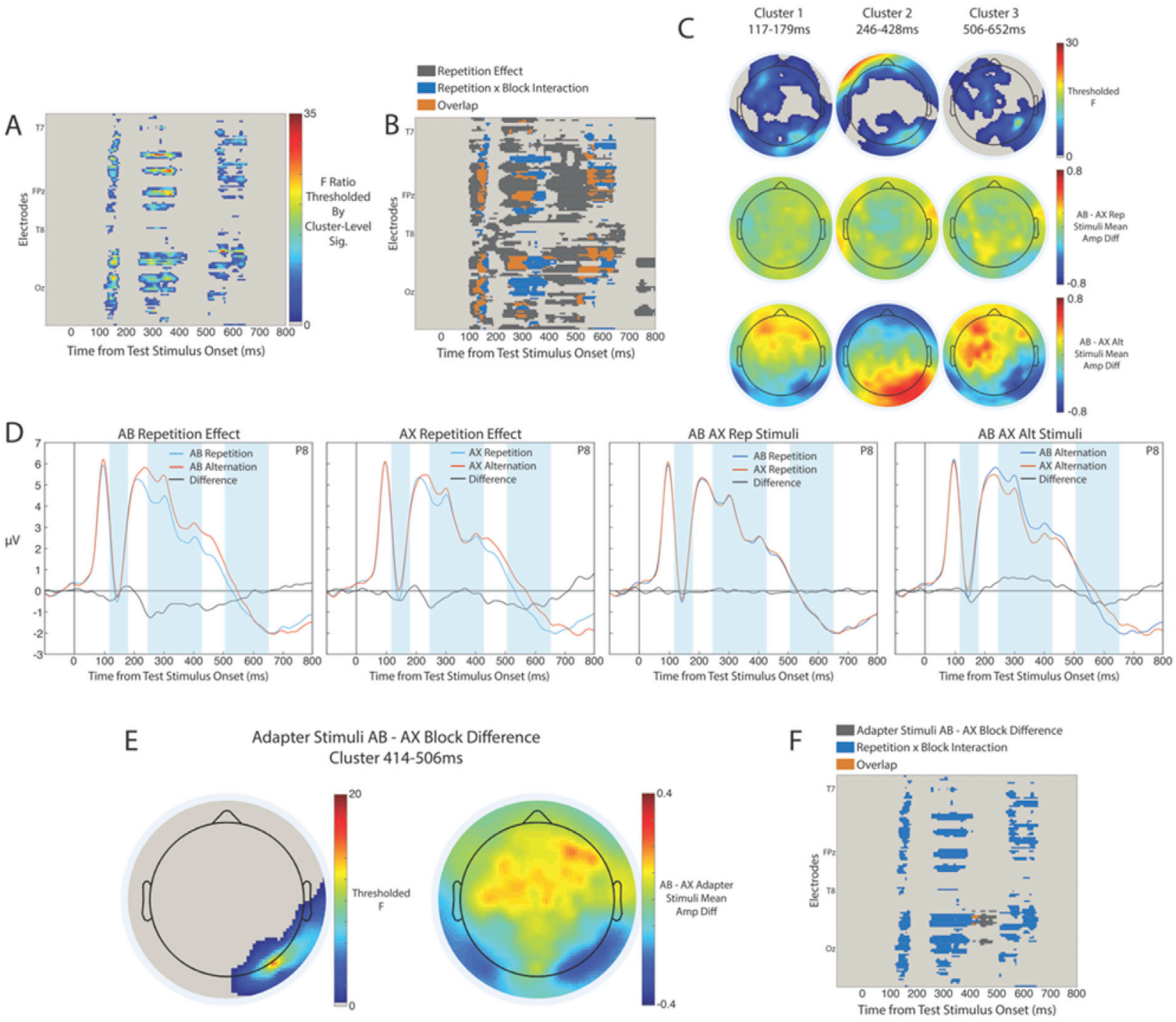

Fig. 5. Results of mass univariate block by repetition interaction analyses. A) Timepoint-by-channel matrix of significant repetition by block interaction effects. F ratios are displayed thresholded by cluster-level statistical significance (F ratios ≤0.55 also changed to grey). B) Timepoint-by-channel matrix of the spatiotemporal overlap of statistically significant repetition effects and block by repetition interactions. C) Scalp maps of repetition by block interaction effects by latency from test stimulus onset. In the top row average F ratios across each time window are displayed for electrodes within statistically significant clusters (F ratios ≤0.47 changed to grey). Average AB - AX amplitude differences are shown for repeated and alternating stimuli in the middle and bottom rows. D) Grand-average ERPs showing repetition effects in AB and AX blocks. Shaded areas correspond to time windows of interaction effects displayed in Fig. 5C. E) Scalp maps of differences between ERPs evoked by adapters in AB and AX blocks (F ratios ≤0.31 changed to grey). F) Timepoint-by-channel matrix of the spatiotemporal overlap of statistically significant adapter AB-AX block differences and test stimulus repetition by block interactions. (two-column fitting image).

extrastriate visual cortex (Kaliukhovich and Vogels, 2011; Meyer et al., 2014a; Kaposvari et al., 2016).

The positive dipole effect of the later (328–375ms) expectation effect in our results matches the topography and latency of stimulus expectation effects in the ERP study of Summerfield et al. (2011). It appears that this expectation effect overlapped with the positive dipole of the N250r repetition effect at central electrodes, leading to the appearance of interactive stimulus repetition and expectation effects in their analysis design. This also explains why no expectation effects were identified at bilateral occipitotemporal channels that capture the negative dipole of the N250r repetition effect (Schweinberger et al., 2002; Schweinberger and Neumann, 2016) which was reported in Summerfield et al. to be modulated by expectation.

Modulations of repetition effects by expectation

ERP repetition and expectation effects did not statistically interact throughout the epoch and showed distinct spatiotemporal patterns of effects, in agreement with previous findings that stimulus repetition effects are distinct from effects of perceptual expectations (Grotheer and Kovacs, 2015; Kaliukhovich and Vogels, 2011, 2014). Together, these findings support models that specify separate repetition and perceptual expectation effects (e.g. Grotheer and Kovacs, 2016; Grimm et al., 2016; Henson, 2016; Vogels, 2016) and provide evidence against models proposing a modulatory effect of perceptual expectation on the magnitude of repetition suppression (Summerfield et al., 2008, 2011; Auksztulewicz and Friston, 2016). Additionally, studies reporting changes in directed connectivity with stimulus repetition consistent with predictive coding models have used designs that confound stimulus repetition and expectation (e.g. Garrido et al., 2009; Ewbank et al., 2011; de Gardelle et al., 2013; reviewed in Auksztulewicz and Friston, 2016). Importantly, these connectivity changes could also plausibly occur from additive repetition and expectation effects. Modelling results from experiments the orthogonally manipulate repetition and expectation are needed to verify whether repetition effects are associated with changes in top-down connectivity.

It is important to note that we cannot directly support the null hypothesis of no expectation by repetition interaction using our frequentist mass univariate testing approach, and that our cluster-corrected analysis approach may have limited our ability to detect effects over small numbers of timepoints and/or electrodes (see Groppe et al., 2011). Future studies could focus on individual repetition effect time windows, and adopt Bayesian hypothesis testing to quantify evidence for null and alternative hypotheses (Rouder et al., 2009). This could be done using priors informed by our study and previous face repetition experiments (for a review of face repetition experiments see Schweinberger and Neumann, 2016). In addition, expectation effect sizes, as found in our study, were small compared to repetition effects, and it is possible that such effects were simply too small to drive a statistically-significant repetition by expectation interaction. Expectation effects on electrophysiological (in contrast to haemodynamic) responses appear to be very small (if present at all) in visual cortex when using similar designs to the current study (e.g. Kaliukhovich and Vogels, 2011). Although expectation effects were larger in Summerfield et al. (2011), this is likely due to their small sample size ($n = 13$), and therefore low statistical power, inflating observed effect sizes (Button et al., 2013; Gelman and Carlin, 2014). However, other sources of information support the claim that repetition effects are not a product of perceptual expectations. The main effects of repetition and expectation in our results had differing topographies and only partially overlapped in time (Fig. 3B), indicating distinct processes. In addition, any differences in point estimates of repetition effects by expectation appeared to be much smaller than the repetition effects themselves (shown in Fig. 3E), contrary to the claim that repetition effects are not found for surprising stimuli (e.g. Summerfield et al., 2008). As our results also explain the reported expectation by repetition interaction in Summerfield et al. (2011) as a mixture of additive effects, it appears that there is currently no electrophysiological evidence of modulations of repetition suppression by expectation, at least for studies using visual stimuli.

Findings of noninteracting repetition and perceptual expectation effects in our study and those of other experiments using electrophysiological recordings (Kaliukhovich and Vogels, 2011, 2014) contrast with reports of larger BOLD repetition effects for surprising stimuli (e.g. Amado et al., 2016; de Gardelle et al., 2013; Larsson and Smith, 2012; reviewed in Kovacs and Vogels, 2014). One possibility is that these BOLD increases to surprising alternations result from increased gamma-band activity (e.g. Todorovic et al., 2011), hypothesised to signal feedforward prediction errors in supragranular cortical layers (Auksztulewicz and Friston, 2016). Gamma-band activity can be closely coupled with the BOLD response (Niessing et al., 2005) but would not be found in the ERPs analysed in our study. Future studies using MEG, electrocorticography or intracranial electrodes will be able to determine whether surprise responses, as reflected in gamma band activity, are suppressed by stimulus repetition.

Differences in repetition effects by block type

Magnitudes of repetition effects differed across AB and AX block types, with stimuli in each block type showing larger repetition effects at distinct latencies from stimulus onset. Block differences were found specifically for alternating stimuli, indicating that block effects did not modulate the underlying repetition effect mechanisms, but rather affected the observed repetition/alternation signal difference (see Feuerriegel, 2016 for further discussion of this issue). Our findings indicate that many previous experiments, which have used predictable repeated stimuli and unpredictable alternating stimuli, may have indexed stimulus predictability effects as part of the observed repetition effect.

We also found differences in adapter stimulus-evoked ERPs between 414 and 506 ms at right posterior electrodes, which did not substantially overlap in time with the test stimulus repetition by block interaction effects. One interesting possibility is that such ERP differences are related to the different types of expectations that could be formed after viewing the adapter stimulus in AB compared to AX blocks. The topography of our effects is consistent with such expectation formation-related effects reported in the right hippocampus and right inferior temporal cortex (Turk-Browne et al., 2010). We caution against making strong claims based on this exploratory analysis, however our results hint that indices of expectation formation could be detected using ERPs.

One limitation of this study is that we could not dissociate novelty and predictability effects in our experimental design. Larger repetition effects in AX blocks likely index effects of both increased novelty for AX alternating stimuli (e.g. Xiang and Brown, 1998; Mur et al., 2010) and the inability to form image-specific expectations for alternating stimulus images in AX blocks (e.g. Hsu et al., 2013, 2014, 2015). Future research controlling for stimulus novelty may be able to identify and isolate stimulus feature predictability effects in repetition designs, which have received little attention in the repetition suppression literature (but see Pajani et al., 2017; Feuerriegel, 2016). In addition, face identities used for AX alternating stimuli were from a different stimulus subset to faces used for adapters, repeated test stimuli and AB block alternating stimuli. Face images were equated for pixel intensity and stimulus contrast across subsets, and faces were randomly assigned to each subset, however it is possible that differences in responses to individual faces in each set may have also contributed to the observed effects. This can be remedied in future work by counterbalancing faces used within each condition.

It is unclear why AB blocks showed larger repetition effects between 246 and 428ms (during the N250r repetition effect). The scalp topography of block differences for alternating stimuli during this time window is different to the effects at earlier and later latencies (shown in Fig. 5C), which indicates a qualitatively-different predictability or novelty effect. One possibility is that this effect arises from altered input to visual regions caused by the earlier block effect, similarly to how stimulus repetition effects are inherited across visual areas (reviewed in Feuerriegel, 2016). Future studies that measure the covariance of expectation effects at different latencies may uncover spatiotemporal patterns of prediction effects to constrain models of how predictions propagate through the visual system. Another possibility is that population responses to the often-presented alternating stimuli in AB blocks became more distinct from those to other faces in inferior temporal areas through repeated stimulus presentation (familiarisation; e.g. Freedman et al., 2006; Meyer et al., 2014b). More distinct population response patterns between faces would lead to less cross-stimulus adaptation of alternating stimuli by visually-similar adapters (Verhoef et al., 2008; De Baene and Vogels, 2010) resulting in larger differences between repeated and alternating stimulus-evoked ERPs.

Conclusions

This research has systematically, and using a data driven approach, identified distinct spatiotemporal sequences of stimulus repetition and expectation effects on ERPs in the one experimental paradigm. Our results support two-stage models of repetition suppression that pose a distinction between repetition effects driven by prior stimulus exposure and perceptual expectations (Grotheer and Kovacs, 2016; Grimm et al., 2016; Henson, 2016; Vogels, 2016).

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