



## Stimulus repetition probability effects on repetition suppression are position invariant for faces

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### ABSTRACT

It has been shown that the probability of face repetitions influences the magnitude of repetition-related response reductions (Summerfield et al., 2008), implying that perceptual expectations affect adaptation and repetition suppression processes in the human central nervous system. An unresolved question is whether probability effects are specific for the retinal position of the stimuli or affect stimulus processing globally, throughout the visual field. To address this question we tested whether face repetition probability affects fMRI adaptation (fMRIa) when the repeated stimuli are presented on the same retinal position, overlapping each other or when they are presented in opposite hemifields. Subjects were exposed to either two identical (repeated trial, RT) or two different (alternating trial, AT) face stimuli. Both types of trials were presented either in blocks consisting of 75% (repeated block, RB) or 25% (alternating block, AB) of RTs. We found that repetition probability influences fMRIa equally for overlapping and nonoverlapping arrangements: the signal reduction after RT was more pronounced in RB than in AB for both spatial arrangements of stimulus-pairs. This effect was present in bilateral fusiform and occipital face areas, as well as in the lateral occipital cortex. Our results support the role of stimulus repetition probability in determining fMRIa and shows that the effect is invariant to the retinal position of stimuli.

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### Introduction

One of the major organizing principles of the mammalian visual cortex is that it has a hierarchical neural network architecture with bottom-up and top-down connections (Rousselet et al., 2004; van Essen et al., 1992). According to models of predictive coding (PC) the top-down connections of this system are tuned to the expected probabilities of certain features or objects (Friston, 2005; Rao and Ballard, 1999; Spratling, 2008), preparing the observer for any unexpected event. A central hypothesis of such PC models is that repeating a stimulus leads to its increased expectation and reduced prediction error (i.e. the neural activity signaling the mismatch between top-down or expected and bottom-up or observed events). The prediction error recalibrates the neural representations continuously and enables the system to code the novel, unexpected stimuli with higher efficiency (Friston, 2005). Indeed, recent functional magnetic resonance imaging (fMRI), magnetoencephalography (MEG) and event-related potential (ERP) studies have confirmed the central role of signal adaptation in

PC in the human central nervous system. First, prolonged adaptation to different facial features, leading to contrastive aftereffects, resulted in different attenuation of the MEG/ERP response from 170 ms onwards, in a relatively late time-window suggesting the involvement of top-down mechanisms (Furl et al., 2007; Kovács et al., 2006). Second, the technique of fMRI adaptation (fMRIa) provided evidence for the involvement of PC in face processing. In fMRIa the repetition of a given stimulus leads to the attenuation of the blood oxygen level-dependent (BOLD) signal when compared to alternating stimuli (Grill-Spector et al., 2006; Krekelberg et al., 2006). Importantly Summerfield et al. (2008) have shown that the magnitude of the fMRIa was significantly larger in the fusiform face area (FFA) in blocks with high probability of facial stimulus repetition than in blocks where repetition was infrequent. This result suggested that the probability of stimulus repetition within a long series of trials affects the magnitude of neural repetition suppression. According to the authors this is due to the fulfilled perceptual expectations of the observer in the case of frequently repeated stimuli (for a review on the difficulty of the separation of expectation and attention effects see Summerfield and Egner, 2009).

However, unlike in the above-mentioned studies where PC was investigated with foveal stimuli and controlled fixation, in everyday life our eyes are continuously moving and thus the retinal position

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of the visual objects is changing from one fixation to the other. Therefore it is an important and unresolved question whether top-down predictive processes are specific or invariant to the actual position of any stimulus. Furthermore, since it is assumed that PC and top-down attentional selection processes might be related (for a review see Larsson and Smith, 2011; Spratling, 2008; Summerfield and Egner, 2009) one can reason that if stimulus probability affects repetition suppression via top-down, feedback connections than this effect might also be insensitive to the location of the stimuli, similarly to the global feature-based attentional selection processes (Boehler et al., 2011; Liu et al., 2007; Liu and Mance, 2011; Melcher et al., 2005; Saenz et al., 2002; Sohn et al., 2005; Zhang and Luck, 2008).

In our current fMRI experiment we tested whether predictability of peripherally presented face stimuli reduces responses in the fusiform face area in a position specific or position invariant manner. To test this we assessed whether repeating a stimulus in opposite hemifields leads to smaller effects of stimulus probability than when the two stimuli are presented within the same hemifield, overlapping each other. From previous studies (Kovács et al., 2008) we know that the fMRI itself is insensitive to the relative position of adaptor and target stimuli in FFA, suggesting position invariant adaptation. Here we asked if a modulation in repetition probability affects fMRIa in a position-specific or position-invariant manner.

In addition we also assessed the specificity of the probability effect to FFA. In their original report, Summerfield et al. (2008) concentrated primarily on the modulation of the response within the FFA. The lack of any modulation of the repetition suppression within the parahippocampal place area, an area involved in the neural processing of houses and scenes (Epstein and Kanwisher, 1998) was interpreted as evidence that the stimulus probability effect is restricted to the face-processing stream. However, models of predictive coding suggest that such modulation should occur in every consecutive processing stage of the visual cortex (Rao and Ballard, 1999) and we know that face processing activates a number of cortical areas (Ishai, 2008; Wiggett and Downing, 2008). Thus, in addition to FFA, here we measured the activity within lower-order areas of the occipito-temporal cortex, involved in shape and face perception as well. Specifically, we tested the occipital face area (OFA) (Gauthier et al., 2000; Haxby et al., 2000; Rossion et al., 2003; Schiltz and Rossion, 2006), an area that previously showed significant fMRIa effects (Kovács et al., 2008), and the lateral occipital cortex (LO) (Grill-Spector et al., 2001; Kourtzi and Kanwisher, 2000), a proposed homologue area of the macaque inferior temporal cortex (IT) (Denys et al., 2004; Sawamura et al., 2006). This later area was of special interest since recent extracellular single-cell recording experiments showed that the IT of the macaque brain lacks any modulation of the neural response due to stimulus repetition probability (Kaliukhovich and Vogels, 2010).

## Materials and methods

### Subjects

Eighteen healthy university students participated in the experiment. Two of them had to be excluded due to technical problems related to the stimulus program. Out of the remaining 16 subjects (mean age: 24.0 yrs, SD: 4.4 yrs) thirteen were female and two participants were left-handed. All participants had normal or corrected-to-normal vision and they provided their written consent in accordance with the protocols approved by the Ethical Committee of the University of Regensburg.

### Stimulation and procedure

Faces were gray-scale, full-front digital photos of 180 female and male faces each, chosen from a large pool of photos of our own and of Minear and Park (2004). Faces (mean luminance: 18 cd/m<sup>2</sup>) were

fit behind a circular mask (radius = 4.2 deg), eliminating outer contours of the faces and were displayed peripherally on a black background, 5.5 deg to the left or to the right of the fixation point, corresponding to a previous study (Kovács et al., 2008). Stimuli were back-projected via an LCD video projector (JVC, DLA-G20, Yokohama, Japan, 72 Hz, 800×600 resolution) onto a translucent circular screen (app. 30 deg. diameter), placed inside the scanner bore at 63 cm from the observer. Stimulus presentation was controlled via Matlab (The MathWorks, Natick, MA, USA), using Psychtoolbox (Version 3.0.8).

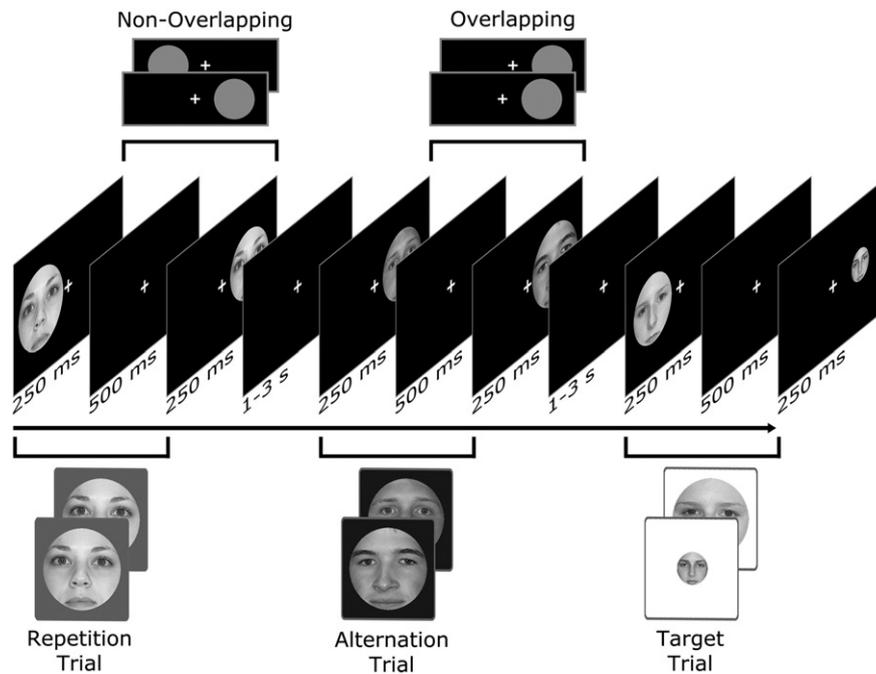
The stimulation paradigm and the structure of trials and blocks were identical to that of Summerfield et al. (2008), with the exception of the number of trials per block, which were twice as many in our study. Stimuli were presented for 250 ms each pairwise, separated by a 500 ms inter-stimulus interval and followed by a 1–3 s long inter-trial interval. The first face (S1) could either be identical to (Repetition trial, RT) or different from the second face (S2, alternation trial, AT). Faces within one trial were always matched for gender. To reduce local feature adaptation and apparent motion cues the size of S1 or S2 was reduced by 15% (radius = 3.6 deg). The visual hemifield of the S1 and S2 images could either be the same, overlapping each other (OL), or they were presented in the opposite hemifields (non-OL), randomly (Kovács et al., 2008). One trial lasted 1 s in each condition. For stimulus examples and trial demonstration see Fig. 1.

Two different types of blocks were presented to the subjects, each repeated three times within a single run (240 trials). The blocks (40 trials each) were separated from each other by a 4 s pause during which the words “New Block” appeared centrally on a black background. In the Repeated Blocks (RB) 60% of the trials was RT while 20% was AT. In the alternation blocks (AB) 60% was AT and 20% RT. The remaining 20% was in both cases target trials such that a target trial could be AT or RT with the same relative probability as the non-target trials and it could be in OL or non-OL arrangement with equal probability. With the exception of the first two trials of a block, which were always the more frequent trials of that specific block (RT in RB and AT in AB), RT and AT were mixed randomly within a block. In addition, the hemifield of S2 (left or right) and the relative spatial arrangement of S1 and S2 images (OL or non-OL) were chosen randomly for both RT and AT. The participant's task was to maintain central fixation throughout a trial and to signal the occurrence of target trials, where the size difference between S1 and S2 was 40% (radius = 1.8 deg) by pressing a button. Participants were given a brief explanation of the task and were given a 1-min presentation to demonstrate the size difference of the target trials prior to scanning. Next, three runs were presented one after the other during one experiment (39 min) for a total of 720 trials. The design of the runs and the structure of the different blocks are presented schematically in Fig. 2.

### Parameters and data analysis

Imaging was performed using a 3-Tesla MR head scanner (Siemens Allegra, Erlangen, Germany). For the functional series we continuously acquired images (34 slices, 10 deg tilted relative to axial, T2\* weighted EPI sequence, TR = 2000 ms; TE = 30 ms; flip angle = 90 deg; 64×64 matrices; in-plane resolution: 3×3 mm; slice thickness: 3 mm). High-resolution sagittal T1-weighted images were acquired using a magnetization EPI sequence (MP-RAGE; TR = 2250 ms; TE = 2.6 ms; 1 mm isotropic voxel size) to obtain a 3D structural scan.

Details of preprocessing and statistical analysis are given elsewhere (Cziraki et al., 2010; Kovács et al., 2008). Briefly, the functional images were corrected for acquisition delay, realigned, normalized to the MNI-152 space, resampled to 2×2×2 mm resolution and spatially smoothed with a Gaussian kernel of 8 mm FWHM (SPM8, Welcome Department of Imaging Neuroscience, London, UK). These preprocessing steps are comparable to those used by Summerfield et al. (2008).



**Fig. 1.** Stimulation parameters and arrangements. A non-overlapping repetition trial (RT, grey), an overlapping alternation (AT, black) and target trial (white) is illustrated with contralateral S2.

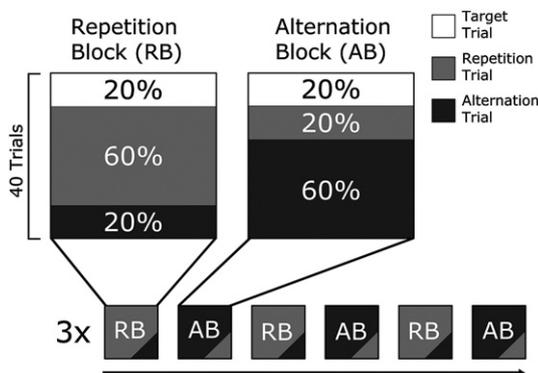
Regions of interests (ROI) analysis was based on the results of separate functional localizer runs (488 s, 17 s epochs of faces, objects and their Fourier randomized versions interleaved with 17 s of blank periods, 2 Hz stimulus repetition rate; 300 ms exposition time; 200 ms blank) and analyzed using MARSBAR 0.42 toolbox for SPM (Brett et al., 2002). To convert the MNI coordinates into the Talairach system we used an open-source algorithm (<https://www2.bc.edu/~slotnic/scripts/mni2tal.m>).

The location of face responsive areas was determined individually as areas responding more strongly to faces than to objects and to Fourier noise images in independent functional localizer scans ( $p_{\text{uncorrected}} < 10^{-6}$ ;  $T = 4.86$ ,  $df = 273$ ), FFA [average Talairach coordinates ( $\pm$  SE): 43(1), -53(2), -28(1) and -45(1), -58(2), -32(1) for left ( $n = 11$ ) and right hemispheres ( $n = 15$ ), respectively] and the OFA [average Talairach coordinates ( $\pm$  SE): 43(1), -77(2), -21(2) and -40(2), -81(2), -22(2) for left ( $n = 13$ ) and right ( $n = 15$ ) hemispheres]. Areas selectively responding to objects were determined by similar functional localizer scans comparing the activity for objects versus their Fourier randomized versions and faces ( $p_{\text{uncorrected}} < 0.000001$ ;  $T = 4.86$ ;  $df = 273$ ). The

object-selective area LO (Grill-Spector et al., 1999, 2001) corresponded to the posterior dorsal portion of the lateral occipital complex (LOC, Malach et al., 1995) [average Talairach coordinates ( $\pm$  SE): 51(1), -73(2), -9(1) and -49(1), -72(2), -8(2) for left ( $n = 14$ ) and right ( $n = 15$ ) hemispheres]. To identify the location of early visual cortex of the right hemisphere ( $n = 16$ ) we calculated the T-maps in the Fourier noise images > faces contrast ( $p_{\text{uncorrected}} < 0.000001$ ;  $T = 4.86$ ;  $df = 273$ , [average Talairach coordinates ( $\pm$  SE): 5(2), -92(1), -6(2)]). The ROIs were selected individually on the single subject level from these thresholded T-maps. Areas matching our anatomical criteria and lying closest to the corresponding reference cluster (based on the results of the previous literature) were considered as their appropriate equivalents on the single subject level. A time series of the mean voxel value within a 4 mm radius sphere around the local peak of the areas of interest was calculated and extracted from our event-related sessions using finite impulse response (FIR) models (Ollinger et al., 2001). The convolution of a reference hemodynamic response function with boxcars, representing the onsets and durations of the experimental conditions, was used to define the regressors for a general linear model analysis of the data.

RT and AT trials were analyzed and modeled at the onset of the S1 stimuli separately (duration = 1 s), following the methods of other studies (Murray and Wojciulik, 2004; Summerfield et al., 2008). Only the non-target trials were modeled and included in the statistical analysis. The peak of the event-related averages in a window from 6 to 8 s was used as an estimate of the magnitude of the response and was averaged across observers. We performed three-way within-subject ANOVAs on the peaks activations with block type (2: RB, AB), trial type (2: RT, AT) and spatial arrangement of S1 and S2 (2: OL, non-OL) as factors for each area and for the ipsilateral and contralateral S2s separately. Post-hoc analysis was performed by Fisher LSD tests.

To compare the magnitude of repetition suppression of OL and non-OL conditions directly we performed the following additional analysis. First we calculated a repetition suppression index score (RSI) following the methods of (Axelrod and Yovel, 2011; Kaliukhovich and Vogels, 2010) using the equation  $RSI = (R_{\text{alt}} - R_{\text{rep}}) / (|R_{\text{alt}}| + |R_{\text{rep}}|)$  where  $R_{\text{alt}}$  and  $R_{\text{rep}}$  are the average responses in the AT and RT within



**Fig. 2.** The composition of the repetition (RB) and alternation blocks (AB). During a run RB and AB were alternating, each repeated three times. Three such runs were recorded for each subject.

a given block and position condition, respectively. Positive values indicate more pronounced responses in the AT than in the RT, negative values indicate the opposite while zero values indicate the absence of any response differences between the two trial types.

## Results

Participants detected the occurrence of target trials on average with 90.6 and 89.7% (1.3 and 1.0% ± SE) accuracy in the RB and AB conditions, respectively. Informal questioning of the subjects after the experiments revealed that none of them was aware of the manipulation of the repetition probability between blocks.

### Responses to contralateral S2

#### Right hemisphere

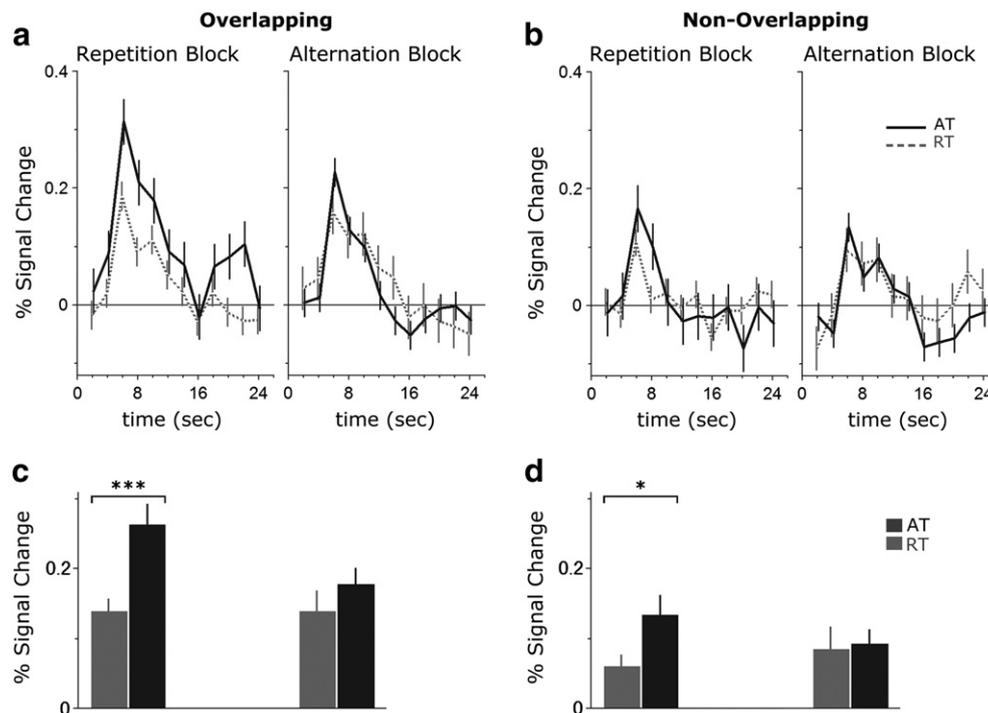
With respect to the contralateral (i.e. left hemifield) S2 presentations in the rFFA (Fig. 3) our results are similar to those of Summerfield et al. (2008). We found significantly larger BOLD signal for AT compared to RT (main effect of trial type:  $F(1,87) = 20.1, p < 0.0001$ ). The magnitude of repetition suppression was more pronounced in the RB than in the AB, as suggested by the block type × trial type interaction ( $F(1,87) = 8.4, p < 0.005$ ). This was largely due to the fact that for the OL condition the AT led to greater overall responses in the RB than in the AB (post-hoc test for AT in RB vs AB:  $p < 0.01$ ), which is different from the results of Summerfield et al. (2008) who reported similar activations evoked by AT in RB and AB. In addition, OL and non-OL conditions led to significant differences (main effect of position:  $F(1,87) = 20.9, p < 0.0001$ ), OL stimulus pairs leading to larger BOLD signal than non-OL. In order to be comparable to Summerfield et al. (2008), we followed their methods and modeled the hemodynamic response at the onset of S1. The fact that we found larger responses for OL than for non-OL suggests (in spite of the limited temporal resolution of fMRI) that the neural response of S1 and S2 is integrated temporally more sufficiently in the OL

than in the non-OL condition. Neither the main effect of block type, nor any other interaction was significant. These results clearly show that we can observe repetition suppression in the RBs for both the OL and non-OL stimuli (Fisher's post-hoc test:  $p < 0.0005$  and  $p < 0.05$ , respectively), suggesting positional invariance.

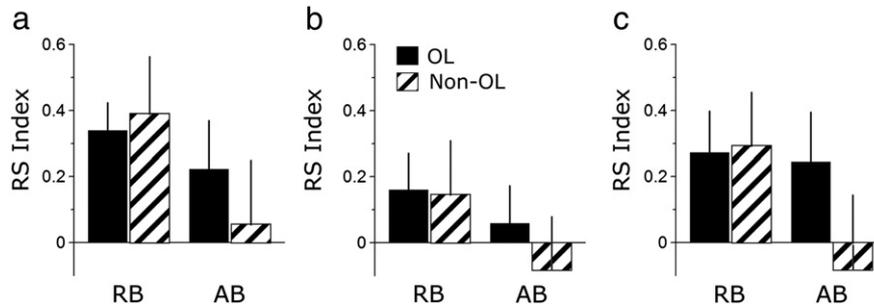
To compare the repetition suppression of the OL and non-OL S1/S2 conditions directly we performed a two-way ANOVA on the RSI (see methods) with position (2) and block type (2) as within-subject factors (Fig. 4a). This analysis revealed, in addition to the significantly larger RSI in the RB than in the AB (main effect of block type:  $F(1,14) = 4.6, p < 0.05$ ) neither a significant main effect of position ( $F(1,14) = 0.1, p = 0.73$ ) nor a significant interaction of block type and position ( $F(1,14) = 0.3, p = 0.58$ ). These results support further the conclusion that the observed repetition suppression in the rFFA is position invariant.

Essentially the same results were found for the two other occipito-temporal areas of the right hemisphere, OFA (Fig. 5a) and LO (Fig. 5b). The main effect of trial type (OFA:  $F(1,95) = 9.8, p < 0.005$ , LO:  $F(1,89) = 6.1, p < 0.05$ ), superseded by the significant interaction of trial and block types (OFA:  $F(1,95) = 8.4, p < 0.0005$ , LO:  $F(1,89) = 8.14, p < 0.01$ ) shows similar repetition suppression in both areas. Surprisingly and in spite of the main effect of position ( $F(1,95) = 38.9, p < 0.0001$  for OFA and  $F(1,89) = 26.1, p < 0.0001$  for LO) the observed repetition suppression was also position-invariant both in OFA and LO. Post-hoc comparisons confirmed that the response reduction due to stimulus repetition was present in the RBs of both the OL ( $p < 0.002$  for OFA and  $p < 0.01$  for LO) and non-OL conditions ( $p < 0.05$  for both OFA and for LO). Similarly to FFA, AT led to significantly larger responses in the RB than in the AB for both areas (OFA:  $p < 0.05$  for both OL and non-OL, LO:  $p < 0.05$  for OL).

The direct comparisons of the RSIs in the OL and non-OL conditions (Fig. 4b, c) revealed neither a significant main effect of position (rOFA:  $F(1,15) = 0.3, p = 0.59$ , rLO:  $F(1,14) = 3.2, p = 0.09$ ) nor a significant interaction of block type and position ( $F(1,14) = 0.71, p = 0.41$ ). These results support further the conclusion that the observed repetition suppression in the rOFA and rLO is also position invariant.



**Fig. 3.** Time course (mean ± standard error) of fMRI activity in the right FFA for contralateral S2 visual presentations during overlapping (a) and non-overlapping (b) trials. Data derived from a finite impulse response (FIR) model with 2 s time bins. Average peak activation profiles (± standard error) of the right FFA for the overlapping (c) and non-overlapping conditions (d). AT—alternation trials, RT—repetition trials. \*\*\*Fisher's post-hoc comparisons:  $p < 0.001$ . \* $p < 0.05$ .



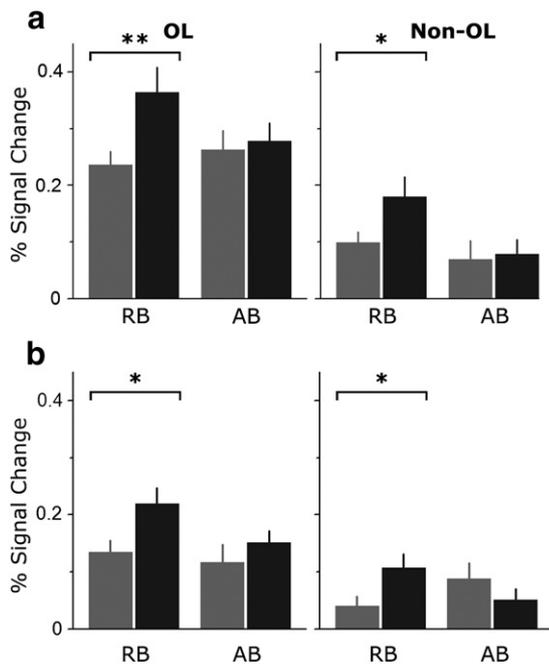
**Fig. 4.** The Repetition Suppression Index (RSI, see methods) for the rFFA (a), rOFA (b) and rLO (c). OL—overlapping condition, non-OL—non-overlapping condition.

#### Left hemisphere

The FFA of the left hemisphere showed a similar, but somewhat more noisy response pattern for contralateral (i.e. right hemifield) S2 compared to that for the rFFA (Fig. 6a). Repetition suppression was observed as a tendency (Fishers post-hoc test:  $p < 0.1$ ) in the OL condition of the RBs while we observed enhancement of the response in the RT of the non-OL RB conditions (Fishers post-hoc test:  $p < 0.05$ ). However, the only significant main effect was due to the significantly lower BOLD responses in the non-OL than in the OL condition (main effect of position:  $F(1,32) = 12.4$ ,  $p < 0.005$ ). The unequal repetition suppression in the RBs of the two position conditions was marked by a significant three-way block type  $\times$  trial type  $\times$  position interaction ( $F(1,32) = 5.2$ ,  $p < 0.02$ ). No other effects were significant.

The left OFA showed no response reduction in the RTs of neither blocks (Fig. 6b). The only significant effect being a significantly lower response in the non-OL than in the OL condition (main effect of position:  $F(1,41) = 20.5$ ,  $p < 0.0001$ ).

Finally, the left LO (Fig. 6c) showed similar responses to the lOFA: we observed a significant main effect of position ( $F(1,41) = 11.5$ ,  $p < 0.005$ ) and a three-way interaction of block type  $\times$  trial type  $\times$  position ( $F(1,41) = 4.1$ ,  $p < 0.05$ ).



**Fig. 5.** Contralateral S2 effects in the right hemisphere. Average peak activation profiles ( $\pm$  standard error) of the right OFA (a) and for the right LO (b) for the overlapping and non-overlapping conditions. AT—alternation trials, RT—repetition trials. AB—alternation blocks, RB—repetition blocks. \*\*Fishers post-hoc comparisons:  $p < 0.01$ . \* $p < 0.05$ .

#### Responses to ipsilateral S2

##### Right hemisphere

We did not observe any significant response for the ipsilateral (i.e. right hemifield) S2 in the OL condition from the rFFA and rOFA (Fig. 7a, b). The main effect of position (rFFA:  $F(1,43) = 6.61$ ,  $p < 0.05$ , rOFA:  $F(1,47) = 19.2$ ,  $p < 0.0001$ ) suggests that the contralateral S1 in the non-OL condition, however, led to a small but significant response. This main effect was superseded by the block type  $\times$  trial type interactions for the rFFA ( $F(1,43) = 6.1$ ,  $p < 0.05$ ) and block type  $\times$  trial type  $\times$  position interaction in the rOFA ( $F(1,47) = 5.8$ ,  $p < 0.02$ ), due to the larger responses in the RT than in the AT during the RB/non-OL condition (OFA: Fishers post-hoc test:  $p < 0.05$ ). No other effect was significant, suggesting that ipsilateral presentation did not lead to repetition suppression.

In the rLO (Fig. 7c) we did not observe any significant responses for ipsilateral stimuli, supporting previous results showing smaller receptive fields, biased strongly towards the contralateral visual hemifield. The significant main effect of position ( $F(1,44) = 6.2$ ,  $p < 0.02$ ) suggests that contralateral S1 in the non-OL condition however, led to a somewhat increased signal. The fact that no other effect was significant suggests, similarly to rOFA and rFFA, that ipsilateral presentation does not lead to repetition suppression in rLO.

##### Left hemisphere

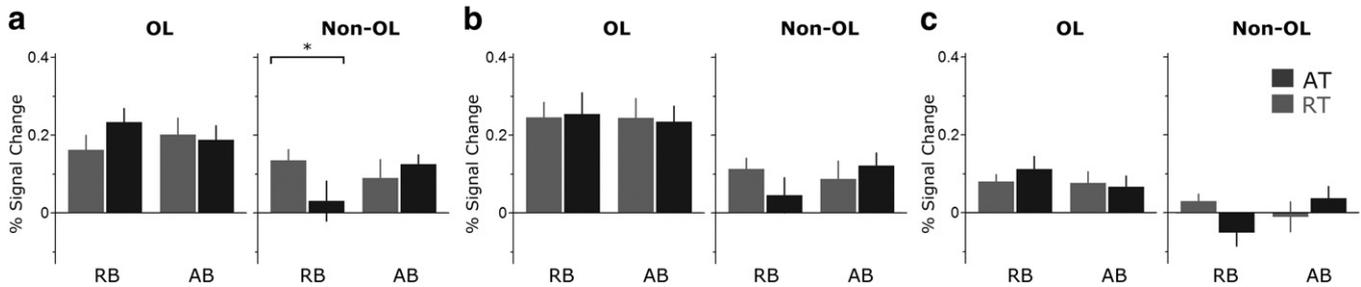
Ipsilateral (i.e. left hemifield) stimulation led to no measurable BOLD signal changes in any of the areas neither in the OL nor in the non-OL conditions.

##### Early visual areas

We analyzed the early visual areas, determined by a Fourier noise images  $>$  faces contrast (Fig. 8). The only difference was a significant main effect of position (contralateral S2:  $F(1,47) = 18.4$ ,  $p < 0.0001$ , ipsilateral S2:  $F(1,47) = 19.3$ ,  $p < 0.0001$ ) suggesting larger responses in the OL than non-OL condition for the contralateral S2 and larger responses in the non-OL than in the OL for the ipsilateral S2. In case of ipsilateral S2 this main effect was significant as well as the three way interaction trial type  $\times$  block type  $\times$  position ( $F(1,47) = 4.2$ ,  $p < 0.05$ ) due to the increased response in the RT than in the AT during the RB/non-OL conditions (Fishers post-hoc test:  $p < 0.001$ ). This pattern of results suggests no repetition suppression in the early visual cortex for face stimuli.

#### Discussion

Our results clearly show that the modulation of repetition suppression by the repetition probability is independent of the relative position of S1 and S2, suggesting position invariant mechanisms of stimulus probability effects. Another important conclusion of the current study is that the modulation of the repetition suppression effect



**Fig. 6.** Contralateral S2 effects in the left hemisphere. Average peak activation profiles ( $\pm$  standard error) of the left FFA (a), left OFA (b) and for the left LO (c) for the overlapping and non-overlapping conditions. AT—alternation trials, RT—repetition trials. AB—alternation blocks, RB—repetition blocks. \* $p < 0.05$ .

is not limited to the fusiform face area, but occurs also in the earlier occipito-temporal cortical areas of the human brain.

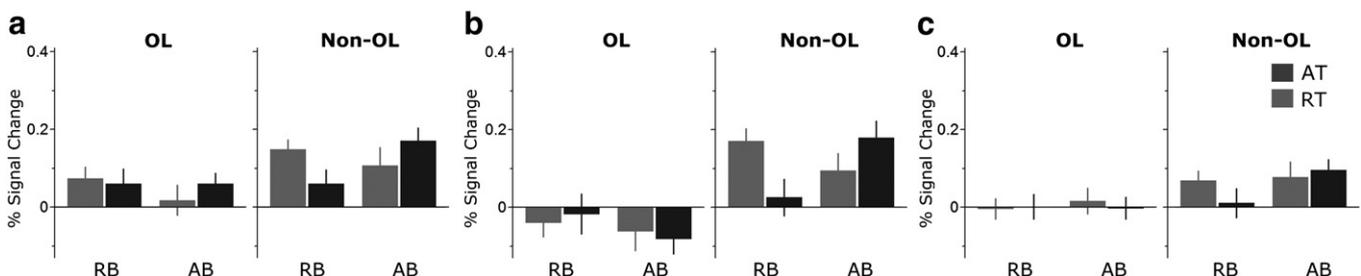
The fusiform face area (FFA) is a central area of the cortical face processing network (for a summary see Kanwisher and Yovel, 2006). This area has been shown to be invariant to the position of the stimuli (Andrews and Ewbank, 2004; Grill-Spector et al., 1999) and fMRIa has recently also been found to be independent of the relative position of stimuli (Kovács et al., 2008). In the current experiments we found evidence for the modulation of fMRIa by stimulus repetition probability for both overlapping and non-overlapping stimuli. This result is in accordance with original models of predictive coding which assumes that higher levels of processing hierarchy operate at larger scales, due to converging lower-level inputs to a higher-level unit, with receptive fields presumably covering the entire visual field (Rao and Ballard, 1999). Being at the top of the face-processing hierarchy, FFA fulfills these criteria, showing repetition probability effects on fMRIa in a position invariant manner. Our results also show, for the first time, that the modulatory effect of stimulus probability, comparable to the effect of feature-based attention (Boehler et al., 2011; Liu and Mance, 2011; Saenz et al., 2002; Sohn et al., 2005; Zhang and Luck, 2008) is also insensitive to the relative position of the repeating stimuli.

However, it is worth mentioning that the observed fMRIa was not entirely position invariant in FFA: we observed very low BOLD responses and no adaptation at all for ipsilateral S2 stimuli. This result contrasts strongly with a previous face adaptation result, showing fMRIa for the ipsilateral target stimuli in FFA as well (Kovács et al., 2008). One possible explanation of the different results is that while we used a large number of trial-unique stimuli in the present study, only a limited number of adaptor and target stimuli were used repeatedly in the previous study. Nevertheless, the role of stimulus number and repetition in determining fMRIa requires further systematic studies.

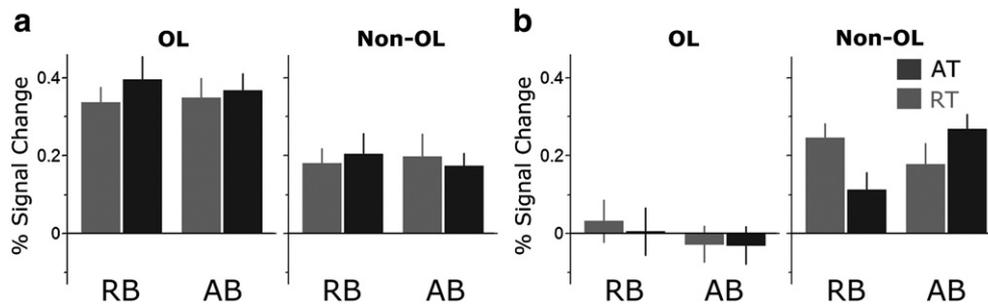
One aspect of predictive-coding theories is that it is not unique to a given cortical area, but rather it occurs concurrently across the levels of cortical hierarchy (Friston, 2005; Friston and Kiebel, 2009; Rao and Ballard, 1999). Thus, it was surprising that one study (Summerfield et al., 2008) found only moderate modulations of the

fMRIa outside the FFA. They described a small cluster of voxels in the area of primary visual cortex being sensitive to the modulation of repetition probability and no such effect in the parahippocampal place area (PPA). We did not observe fMRIa within the early visual areas (defined by separate localizers using the Fourier noise images > faces contrast). This result can be due to the fact that while Summerfield et al. (2008) presented the stimuli centrally, our stimuli were 5.5 deg in the periphery, thereby suggesting different adaptation properties of the central and peripheral representations within the early visual areas. However, since we did not perform quantitative retinotopic mapping our early visual area likely included other visual areas as well, hence the issue requires further testing.

Since the PPA is largely involved in the neural processing of houses and scenes (Epstein and Kanwisher, 1998) one might conclude that the lack of any modulation on the fMRIa within this area means that the effect is limited to the face processing network. However, closer inspection of the data of Summerfield et al. (2008), (Supplementary Fig. 2) reveals that their stimuli did not lead to any enhancement of the BOLD signal in PPA (in fact PPA showed a slight negative BOLD response), suggesting only very weak or no neural responses at all. This result is in accordance with the fact that the PPA is known to respond considerably more to buildings and scenes than to faces (Epstein and Kanwisher, 1998). Some studies found no differences in response of PPA evoked by intact and Fourier-scrambled faces emphasizing the role of low level features in determining the response of PPA (Andrews et al., 2010; Rajimehr et al., 2011). Moreover, recent studies found no traces of fMRIa for repeated faces or houses in PPA either (Andrews et al., 2010). Hence it is not surprising that repetition probability had no effect in the area. Overall, these results question the relevance of PPA as a control area for face repetition related phenomena and suggest that it is still an open question if other areas of the face processing network show similar modulations of the fMRIa to that found in FFA. Our results clearly show similar modulations in FFA and in upstream areas such as the OFA and LO and this supports that models of predictive coding do apply to several processing stages of the ventral visual cortex (Rao and Ballard, 1999). This result is in line with a recent study by Larsson and Smith (2011) who used long adaptation durations and found that



**Fig. 7.** Ipsilateral S2 effects in the right hemisphere. Average peak activation profiles ( $\pm$  standard error) of the right FFA (a), right OFA (b) and for the right LO (c) for the overlapping and non-overlapping conditions. AT—alternation trials, RT—repetition trials. AB—alternation blocks, RB—repetition blocks.



**Fig. 8.** Early visual areas. Average peak activation profiles ( $\pm$  standard error) of the early visual areas for the overlapping and non-overlapping conditions for contralateral (a) and ipsilateral (b) S2 stimulation. AT—alternation trials, RT—repetition trials, AB—alternation blocks, RB—repetition blocks.

stimulus expectation influences fMRI repetition suppression throughout many areas of the visual cortex, as long as subjects attended to the stimuli.

The Larsson and Smith (2011) study has underlined the role of attention in the observed probability dependency of repetition suppression as well. In their study when subjects' attention was diverted away from the stimuli significant repetition suppression was observed but the effect of stimulus probability (and hence the presumed expectation effect) disappeared completely. The relationship of attention to predictive processes remains for the time being unclear. For example, while predictive coding mechanisms generally suggest suppression of the neural responses (Alink et al., 2010; Rao and Ballard, 1999; Summerfield et al., 2008) spatial and feature-based attention are thought to facilitate neural responses (for a review see Carrasco, 2011) and the reconciliation of the two effects in a single model has just begun (Spratling, 2008, 2010). Thus it is an open question if the observed probability effects reflect global attention or expectation processes. In the current study we aimed at studying the position-specificity of the previously observed probability effects on repetition suppression and our experiments were not designed to separate the possible effects of prediction from those of attention. Such future studies will certainly help us understand further the role of stimulus probability in perception.

Interestingly, a recent study (Kaliukhovich and Vogels, 2010), using the same paradigm as Summerfield et al. (2008), found no effect of repetition probability on the adaptation of macaque inferior-temporal (IT) neuronal activity. This is surprising, since IT is regarded as a possible non-human homologue of the area LO (Denys et al., 2004; Sawamura et al., 2006) where we found strong modulations of the fMRIa. What can be the reason of the different results regarding repetition probability modulations in IT and LO? Obvious differences are the experimental species, the stimulus category (faces vs. objects) and the applied methods. As Kaliukhovich and Vogels (2010) argue, only explicit tests of these factors, such as monkey fMRI experiments or explicit comparisons of the probability effects for different stimulus categories could decide which one these differences can explain the opposite results. Our present results, regarding the similar position invariant modulation of repetition suppression by repetition probability in LO suggests that the effect of expectation is manifest across a wide range of occipito-temporal areas for faces and is not necessarily restricted to the core face-processing network.

While our findings are to a large extent in agreement with the results of Summerfield et al. (2008) regarding the effects of repetition probability on FFA signal adaptation there are considerable differences between the results of the previous and the present study. One such difference regards the repetition suppression, observed in the alternation blocks (AB): while Summerfield et al. (2008) found a small but significant reduction in this condition we only observed a small, non-significant reduction in the AB. Since we used trial structures and probabilities identical to those of Summerfield et al. (2008) with even longer blocks (which presumably increases any effect of expectation) this difference can only be due to the different position of stimuli in the two studies: central vs. peripheral.

Another, apparent deviation from the study of Summerfield et al. (2008) is that in the OL conditions (despite the lack of a main effect of block) we observed stronger BOLD signals in alternation trials within the repetition blocks than within the alternation blocks. While this result is clearly in contradiction with the results of the first experiment of Summerfield et al. (2008) where the target stimulus was an upside-down face, closer inspection of their Fig. 2C reveals a similar pattern of activation during their second experiment where the target trials (identical to the task of the present study) included size-deviant upright faces. The response difference between AT/RB vs. AT/AB was of similar magnitude to the repetition suppression of the AB (i.e. the larger response during AT/AB when compared to RT/AB). A simple explanation of the larger AT responses within RB compared to AT responses in AB can be that the violation of predictions leads to stronger BOLD responses. The less frequent ATs within a RB violate predictions, increasing prediction-error response amplitudes (Rao and Ballard, 1999). Indeed, such effects have recently been described in V1, FFA and the hippocampus (den Ouden et al., 2009; Egner et al., 2010; Strange et al., 2005). But why do we not observe similar enhancements then in the inverse situation (i.e. larger responses in RT/AB when compared to AT/AB)? The answer simply can be that the image repetition related suppression of the BOLD response and the surprise related elevations of the response counteract each other. The reduced magnitude of repetition suppression within AB argues for such an explanation.

In conclusion, our results suggest that for face stimuli the repetition probability effects on the fMRIa are not restricted to the fusiform face area, rather they can be observed in the occipital face area as well as in the lateral occipital cortex. Further, in all these areas the effect is to a large extent invariant to the relative position of the stimuli, supporting the top-down nature of the probability effect.

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