Effect of spatial attention on stimulus-specific haemodynamic repetition effects

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The aim of this fMRI study was to investigate whether spatial attention to the initial and/or repeated presentation of a stimulus is necessary to observe repetition-related modulations of the neural responses evoked by that stimulus. During each trial, two stimuli were presented simultaneously, one left and one right of fixation. During each block, participants were instructed to attend covertly to stimuli in one of the two hemifields and respond whether each was a face or house, ignoring the contralateral stimulus. Regions that preferred one stimulus category over the other, such as the fusiform face area and parahippocampal place area, showed evidence of some processing of the ignored stimuli. However, a reduced response to repeated stimuli (repetition suppression) was only reliable for preferred stimuli when both their initial and repeated presentations were attended. This suggests that attention is necessary for both the acquisition and expression of the neural mechanisms that underlie repetition suppression, at least over the lags of 2–16 intervening trials used here.
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The repetition of a stimulus, even after several intervening different stimuli, often produces a decreased neural response in brain regions associated with processing that stimulus (Grill-Spector et al., 2006). This so-called "repetition suppression" suggests that a single stimulus exposure can engender some form of plasticity that alters the brain's response to that specific stimulus when it is re-exposed. The question addressed here is whether attention needs to be directed to the stimulus for this plasticity to occur (on its initial presentation), or for the effects of that plasticity to be expressed (on its repeat presentation).

Previous fMRI studies on related questions appear to give mixed answers. In two previous fMRI experiments (Eger et al., 2004; Thoma and Henson, in press), we manipulated spatial attention to the initial presentation of the line-drawing of an object. Despite finding reliable repetition suppression in lateral occipital and fusiform regions when the initial presentation was attended, we failed to find evidence of repetition suppression when the initial presentation was ignored. This was despite the fact that the second

presentation occurred only a few seconds later. Using an object-based rather than spatial-based manipulation of selective attention, in which stimuli were superimposed images of a face and a house, two experiments by Yi and colleagues (Yi and Chun, 2005; Yi et al., 2006) also failed to find any evidence of repetition suppression when stimuli were ignored.

However, Bentley et al. (2003) manipulated spatial attention and reported repetition suppression in lateral occipital cortex that was common to faces attended on both first and second presentation and faces ignored on both presentations. Vuilleumier et al. (2005) manipulated object-based attention and found repetition suppression in anterior fusiform regions for objects that had been ignored on their initial presentation. Finally, Murray and Wojciulik (2004) presented objects around a fixation point and directed attention to either the object or to the fixation point. Though reduced, repetition suppression for an object repeated in the same orientation, when measured relative to an object repeated in a different orientation, was still reliable even when attention was directed to the fixation point.

Given this ambiguity, we sought further evidence on this question using spatial attention to bilateral displays of faces and houses (Fig. 1). On each trial, two different images were presented simultaneously for 200 ms, one left and one right of fixation, arranged as face–face, face–house, house–face or house–house. During a block of trials, participants were instructed to attend to images on one side of central fixation, to which they made a simple face/house categorisation decision. On some trials, one of the images, either the attended or the ignored image, had been presented on a previous trial within the same block as either an attended or ignored image. Thus the core of the design was a 2×2 factorial manipulation with conditions (initial–repeat): attended–attended, attended–ignored, ignored–attended and ignored–ignored. In order to match the stimulus configuration, the repetition effect was measured by contrasting trials containing a repeated image with controls trials matched in every respect except that each image was novel. In the ignored–attended condition, for example, trials in which a previously ignored face was presented in the attended hemifield, together with a house in the ignored hemifield, would be contrasted against control trials in which a novel face was attended while a house was ignored (e.g., the two trials outlined in yellow in Fig. 1). The further factors added to this basic design were: (1) category of the critical stimulus (face or

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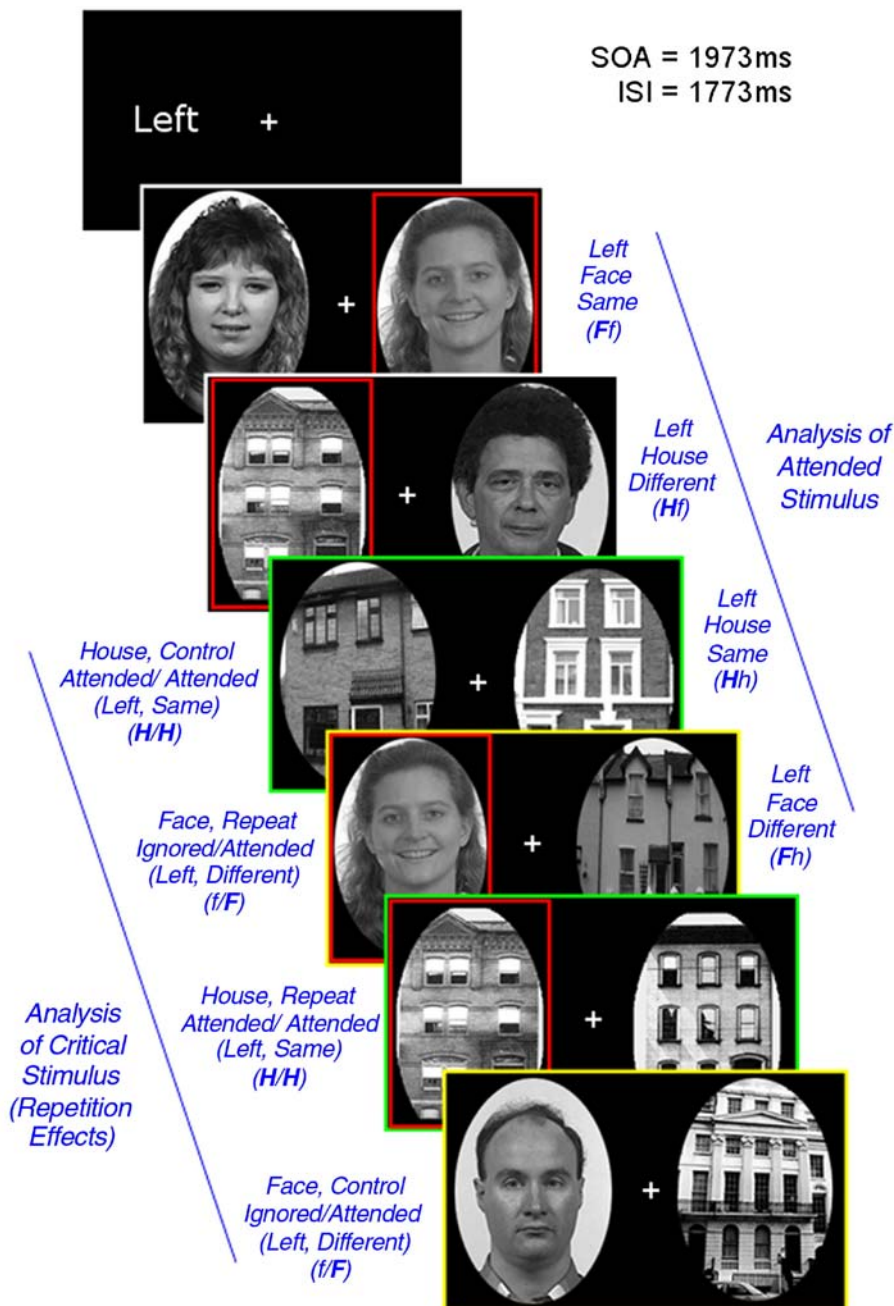 **Available online on ScienceDirect (www.sciencedirect.com).**

Fig. 1. Schematic of experimental design. The red box around a stimulus indicates a repeated stimulus; the green and yellow boxes around a stimulus-pair indicate matched repeat and control trials, which are contrasted in order to measure repetition effects (coloured boxes not present in experiment).

house), (2) attended hemifield (left or right) and (3) contralateral stimulus-relation (same or different).

Materials and methods

Participants

Eighteen right-handed healthy young volunteers (8 female) with normal or corrected-to-normal vision and no history of neurological disease participated in the study after giving written informed consent. The study was of the type approved by a local research ethics committee (LREC reference 05/Q0108/401).

Materials

The stimuli were greyscale photos of 288 unfamiliar buildings (henceforth termed houses) and 288 unfamiliar faces (half male), cropped to fit inside an oval mask. The faces came from the Facial Recognition Technology (Feret) Database (Phillips et al., 2000); the houses came from various sources on the Internet.

Procedure

An example trial sequence is shown in Fig. 1. On each trial, two stimuli were presented for 200 ms, one left and one right of the

fixation point. The stimuli were either two different faces, two different houses or a face and a house. They were displayed against a black background, projected onto a screen approximately 80 cm behind the participant, which they viewed via a mirror placed above the eyes. The horizontal visual angle of the inner edge of the stimuli was 2°; the outer edge was approximately 4°. Each experimental block contained 1 initial instruction trial (the command "left" or "right" presented on the left or right of the screen respectively) followed by 36 trials, lasting approximately 71 s in total. There were 12 blocks in total, alternating in left/right instructions (with the instruction for the initial block counterbalanced across participants). Eight "baseline" trials occurred between each block of directed attention, in which the bilateral stimuli were blank ovals to which participants alternated left/right key presses. Participants were instructed to keep their eyes on the fixation point in the centre of the screen throughout the experiment. The lag between repeats ranged from 2 to 16 (i.e., there was always at least one trial intervening between trials with a repeated stimulus; no stimulus was repeated across blocks).

As explained in Introduction, the critical trials were divided into repeat and control trials, which were matched in terms of the attended hemifield and the stimulus display (e.g., face–house), differing only in whether the critical stimulus had, or had not, been presented previously in the same block. Thus the second presentation of an image was not necessarily contrasted directly against its first presentation because, for an ignored–attended condition for example, this would mean that a trial in which a previously ignored face was now attended would be contrasted against the trial in which that face was ignored (and in a different hemifield). Note that the assignment of stimuli to repeat/control trials was counterbalanced across participants to remove any effects due to specific images.

The first four trials in each block were fillers that were not included in the events of interest. The remaining 32 trials comprised one example of each combination of the five binary factors: critical stimulus category (face/house), contralateral stimulus-relation (same/different), trial-type (repeat/control), initial condition (attended/ignored) and repeat condition (attended/ignored). The sixth factor of attended hemifield (left/right) was manipulated over blocks. The order of repeat and control trials was pseudorandomised in order to minimise the difference in mean position of repeat and control trials within each block (which was 21.5 and 18.5 respectively).

Participants decided whether the stimulus on the attended side was a face or a house, without moving their eyes. The fixation point momentarily changed from a cross (+) to a circle (o) 200 ms prior to the onset of the images in order to prepare participants and help ensure that their eyes were fixated centrally. The intertrial interval (SOA in this case) was 1973 ms (1.33 TRs; see below).

The experiment was run as a single session lasting 18.5 min. Participants responded by pressing a key with the index finger of either their left or right hand, with both speed and accuracy emphasised. The assignment of hand to response alternated across participants. Participants were told that some stimuli were repeated, but that this did not affect their task. Each participant received some practice prior to scanning.

fMRI acquisition

A 3 T TIM Trio system (Siemens, Erlangen, Germany) was used to acquire 24 T2*-weighted transverse echoplanar (EPI) images (64×64 3×3 mm^2 pixels, TE = 30 ms, flip-angle = 78°) per volume with blood oxygenation level dependent (BOLD) contrast. EPIs

comprised 3 mm-thick, 1.2 mm-gap near-transverse slices, tilted up by approximately 30° at the front to minimise eye-ghosting and posterior lateral inferior temporal susceptibility artefacts. The slices were acquired in an odd–even interleaved descending direction. 750 volumes respectively were collected continuously with a repetition time (TR) of 1480 ms, with the first 10 volumes discarded to allow for equilibration effects. The ratio of SOA to TR ensured that the impulse response was sampled every approximately 500 ms (over trials). An MPRAGE T1-weighted structural image was also acquired for each participant with $1 \times 1 \times 1$ mm voxels using GRAPPA parallel imaging (flip-angle = 9°; TE = 2.99 s; acceleration factor = 2).

fMRI analysis

Data were analysed using Statistical Parametric Mapping software (SPM5, http://www.fil.ion.ucl.ac.uk/spm5.html). Preprocessing of the image volumes included spatial realignment to correct for movement followed by spatial normalisation to Talairach space, using the linear and nonlinear normalisation parameters estimated from warping each participant's structural image to a T1-weighted template image from the Montreal Neurological Institute (MNI). These re-sampled images (voxel size $3 \times 3 \times 3$ mm) were smoothed spatially by a 8 mm FWHM Gaussian kernel (final smoothness approximately $11 \times 11 \times 11$ mm).

Statistical analysis was performed in a two-stage approximation to a Mixed Effects model (Holmes and Friston, 1998). In the first stage, neural activity was modelled by a delta function at stimulus onset. The ensuing BOLD response was modelled by convolving these delta functions with a canonical HRF (Friston et al., 1998). The resulting timecourses were downsampled at the midpoint of each scan to form regressors in a General Linear Model. Separate regressors were modelled for the 64 conditions of interest (conditional on correct responses), plus three additional regressors for (1) the hemifield cue at the start of each block, (2) the filler trials at the start of each block, and (3) trials with erroneous responses. To account for some residual artefacts after realignment, the model also included a further six regressors representing the estimated movement parameters, plus an additional regressor for each scan identified as an outlier (defined as a scan containing a slice in which the voxel mean or variance was more than 6 standard deviations of the average mean/variance for that slice across scans). Voxel-wise parameter estimates for these regressors were obtained by maximum-likelihood estimation, using a temporal high-pass filter (cut-off 128 s) to remove low-frequency drifts, and modelling temporal autocorrelation across scans with an AR(1) process (Friston et al., 2002).

Images of contrasts of the resulting parameter estimates comprised the data for one of two second-stage models (see below), analogous to factorial analyses of variance (ANOVAs), which treated participants as a random effect. Within these models, Statistical Parametric Maps (SPMs) were created of the *T* or *F*-statistic for the various ANOVA effects of interest. These maps were thresholded after correction for multiple comparisons using Random Field Theory (Worsley et al., 1995). Stereotactic coordinates of the maxima within the thresholded SPMs correspond to the MNI template. These coordinates bear a close, but not exact, match to the atlas of Talairach and Tournoux (1988).

Second-stage analyses

Two basic factorial analyses were conducted: (1) an ANOVA on the response to the attended stimulus (versus baseline blocks), with

factors "attended stimulus category" (face vs. house), "attended hemifield" (left vs. right) and "contralateral stimulus-relation" (same vs. different), (2) an ANOVA on repetition effects, i.e., the differential response to control minus repeat trials, with factors "critical stimulus category" (face vs. house), "attended hemifield" (left vs. right), "contralateral stimulus-relation" (same vs. different), "initial condition" (attended/ignored) and "repeat condition" (attended/ignored). Note that these ANOVAs differ in that the critical stimulus in the ANOVA on repetition effects is not necessarily attended (see Procedure) and that their dependent measures (response vs. baseline and response to repeat vs. control trials) are orthogonal.

Both factorial analyses were performed as (1) a "whole-brain" search of every voxel to show a reliable effect after correction for multiple comparisons, and (2) a functional "region of interest" (fROI) analysis of the single voxels that showed maximal statistical differences between faces vs. houses. The whole-brain analyses are advantageous in identifying voxels outside the fROIs, and for allowing for functional variability within the fROIs (see Friston et al., 2006); the fROI analyses are advantageous in allowing further factorial analysis of differential responses across regions, where those regions are defined independently of the effects of interest. For the results reported below, the locations of the fROI were defined from the group-analysis, i.e., reflect the location of common activation across the spatially normalised brains. In the Supplementary data, we perform the same analyses when the fROI were defined separately for each participant, allowing for possible anatomical variability in the functional organisation of different people's brains (Saxe et al., 2006).

The whole-brain ANOVAs used a pooled error, while the fROI analyses (and behavioural analyses) used a partitioned error (Henson and Penny, 2003). The reason for using a pooled error in the whole-brain analyses was to ensure sufficient degrees of freedom that the corrections for multiple comparisons across voxels afforded by Random Field Theory were not overly conservative (Nichols and Holmes, 2002).

Results

Behavioural results

Accuracy was close to ceiling in all conditions (mean=97.3%), so only reaction time (RT) data were analysed. Analysis of the attended stimulus, with factors stimulus category (face/house), attended hemifield (left/right) and contralateral stimulus-relation (same/different), showed only two main effects to be reliable: that of stimulus category, $F(1,17)=12.6$, $p<0.005$, and that of contralateral stimulus-relation, $F(1,17)=4.78$, $p<0.05$: Participants responded faster to faces ($M=567$ ms) than houses ($M=589$ ms), and faster when the same stimulus category was presented to left and right hemifields ($M=575$ ms) than when the stimulus categories differed ($M=581$ ms).

The analysis of repetition effects for the critical stimulus (control minus repeat trials), with factors stimulus category (face/house), attended hemifield (left/right), contralateral stimulus-relation (same/different), initial condition (attended/ignored) and repeat condition (attended/ignored) showed only one reliable effect, namely the three-way interaction between stimulus category, initial condition and repeat condition, $F(1,17)=6.47$, $p<0.05$. However, follow-on two-way ANOVAs for faces and houses separately, with factors of initial and repeat condition (collapsing across attended hemifield and contralateral stimulus-relation), showed no reliable effects, $F(1,17)<2.77$, $p>.11$, making interpretation of the three-way interaction unclear. None of the eight basic conditions across

these two separate ANOVAs showed reliable repetition effects, $t(17)<1.87$, $p>0.08$. The lack of reliable priming effects is not surprising given the ease of this particular task. Summary measures of the RTs are given in the Supplementary data.

fMRI results

Localising contrasts: whole-brain analysis

Planned t-contrasts were performed for faces versus houses and houses versus faces within the three-way ANOVA of the attended stimulus. When thresholded for 10 contiguous voxels at $p<0.001$ uncorrected (Table 1; see also Fig. 3), these SPMs revealed the expected bilateral midfusiform and right lateral occipital regions relatively more active for faces (most likely corresponding to the fusiform face area, FFA, Kanwisher et al., 1997, and occipital face area, OFA respectively, Gauthier et al., 2000), and bilateral parahippocampal regions relatively more active for houses, most likely corresponding to the parahippocampal place area (PPA; Epstein et al., 1999), in addition to bilateral regions in middle occipital gyrus and posterior cingulate. These tests were used as functional localising contrasts within the same experimental session (Friston et al., 2006) in order to define voxels that preferred either faces or houses, with the corresponding thresholded image used for small-volume correction (SVC; Worsley et al., 1995) of subsequent orthogonal effects.

Analysis of attended stimulus: whole-brain analysis

In the whole-brain analysis, only effects that survived $p<0.05$, two-tailed, corrected for the whole-brain, or for either of the two stimulus-specific localiser images, were considered. No regions showed evidence of a three-way interaction between attended stimulus category, attended hemifield, and contralateral stimulus-relation.

The two-way interaction between attended stimulus category and contralateral stimulus-relation survived correction for the face localising contrast in a right occipital region and for the house localising contrast in bilateral parahippocampal cortex (Table 2; Fig. 2A). In the parahippocampal cortex, houses produced greater activity when presented in both hemifields than when presented in the attended hemifield alone (see ahead to Figs. 3G and H). Furthermore, houses produced greater parahippocampal activity when presented in the ignored hemifield than when not presented at all (i.e., when two faces were presented; see ahead to Figs. 3E and F).

The two-way interaction between stimulus category and attended hemifield survived correction for the face localising contrast in a

Table 1

Main effect of stimulus category in analysis of attended stimulus (functional localising contrast), t-tests, $p<0.001$, 10 voxels, *=whole-brain correction

Region	Voxels	MNI coordinates			Z
Faces>Houses					
Right fusiform	63	+42	−45	−21	5.66*
Left fusiform	21	−42	−51	−18	3.88
Right lateral occipital	21	+48	−75	0	3.63
Houses>Faces					
Left parahippocampus	314	−27	−45	−12	11.0*
Right parahippocampus	299	+30	−42	−9	10.6*
Left middle occipital	169	−36	−87	+15	6.24*
Right middle occipital	178	+39	−78	+18	6.31
Left posterior cingulate	16	−18	−57	+12	3.88
Right posterior cingulate	25	+21	−57	+12	4.68*

MNI=Montreal Neurological Institute (template coordinates).

Table 2
Analysis of attended stimulus, F-tests

Region	Voxels	MNI coordinates			Z
Attended stimulus × contralateral relation					
Right lateral occipital	6	+51	−69	+6	3.59[F]
Left parahippocampus	109	−24	−45	−12	5.14[H]
Right parahippocampus	148	+27	−42	−9	4.56[H]
Attended stimulus × hemifield					
Right lateral occipital	10	+48	−75	+3	2.98[F]
Left parahippocampus	132	−27	−57	−9	5.06[H]
Left middle occipital	125	−33	−90	+9	4.61[H]

[F] SVC for face localising contrast. [H] SVC for house localising contrast.
Stimulus=face/house, hemifield=left/right attention, relation=same/different stimulus category in contralateral hemifield.

right occipital region, and for the house localising contrast in a left parahippocampal region and a left middle occipital region (Table 2; Fig. 2B). In all three cases, the region showed greater response when its preferred stimulus category was present in the contralateral hemifield, even if this was not the attended hemifield (Fig. 2C/D).

No regions survived correction for the interaction between attended hemifield and contralateral stimulus-relation, nor for the main effects of contralateral stimulus-relation or attended hemifield.[1]

Analysis of attended stimulus: fROI analysis

As an independent analysis, the data from the maxima of the face and house localising contrasts for the FFA ($-42 -51 -18$; $+42 -45 -21$) and PPA ($-27 -45 -12$; $+30 -42 -9$) were entered into an ANOVA with factors region (FFA vs. PPA), hemisphere (left vs. right), stimulus category, attended hemifield and contralateral stimulus-relation.[2] The five-way interaction was reliable, $F(1,17)=12.1$, $p<0.005$. This interaction was examined further by two four-way ANOVAs for faces and houses separately.

When the attended stimulus was a face, there was a reliable four-way interaction between region, hemisphere, attended hemifield and contralateral stimulus-relation, $F(1,17)=7.32$, $p<0.05$. This interaction was examined further by two three-way ANOVAs on FFA and PPA separately. For the FFA, the only reliable effect was the main effect of hemisphere, $F(1,17)=7.27$, $p<0.05$, with greater face-related responses in the right than left hemisphere (see Figs. 3A and B). For the PPA, there was a reliable three-way interaction between hemisphere, attended hemifield and contralateral stimulus-relation, $F(1,17)=10.4$, $p<0.005$. However, follow-on analyses on left and right PPA separately showed only a main effect of contralateral stimulus-relation in both cases, $F(1,17)>15.8$, $p<0.001$, plus a main effect of attended hemifield in the right PPA, $F(1,17)=5.75$, $p<0.05$. The main effects of contralateral stimulus-relation reflected greater responses when the contralateral (ignored) stimulus category was different, i.e., a house (see Figs. 3E and F). Interestingly, this effect was driven by a deactivation relative to baseline (i.e., relative to the control trials of blank ovals; error bars are 95% confidence intervals) when the

ignored stimulus was a face, rather than an activation relative to baseline when the ignored stimulus was a house. The main effect of hemifield in right PPA reflected greater responses to attended faces in the right hemifield[3].

When the attended stimulus was a house, the four-way interaction between region, hemisphere, attended hemifield and contralateral stimulus-relation was also significant, $F(1,17)=9.96$, $p<0.01$. When split by region, the FFA showed only a main effect of hemisphere, $F(1,17)=7.99$, $p<0.05$, with greater responses on the right as before, and a main effect of contralateral stimulus-relation, $F(1,17)=7.31$, $p<0.05$, with greater responses when the contralateral (ignored) stimulus category was different, i.e., a face (Figs. 3C and D). For the PPA, there was a reliable three-way interaction between hemisphere, attended hemifield and contralateral stimulus-relation, $F(1,17)=6.70$, $p<0.05$. However, follow-on analyses on left and right PPA showed only a main effect of contralateral stimulus-relation in both cases, $F(1,17)>4.83$, $p<0.05$. This time, the effect reflected greater responses when the contralateral (ignored) stimulus category was the same, i.e., a house (Figs. 3G and H). A similar pattern of results was found when the FFA and PPA were defined on an individual basis, though in this case, there was evidence of processing the category of ignored stimuli when attending to faces in the FFA, as well as in the PPA (see Supplementary data).

Finally, we examined effects of attention when averaging across the four fROIs according to the preferred vs. non-preferred category for each fROI. If ignored stimuli are processed categorically, this would be the most sensitive test yet. When non-preferred stimuli were attended, responses were greater when the ignored stimulus was preferred, $F(1,17)=30.0$, $p<0.001$, though again, this seemed to reflect an absence of deactivation relative to baseline (Fig. 3J). When preferred stimuli were attended, there was also a trend for greater responses when the ignored stimulus was preferred, though this did not reach significance, $F(1,17)=3.20$, $p=.09$ (Fig. 3I).

Analysis of repetition effects: whole-brain analysis

Initial analyses showed no effect of any factor (stimulus category, attended hemifield, contralateral stimulus-relation, initial condition or repeat condition) on repetition effects (repeat vs. control trials) that survived correction for whole-brain analyses, or survived correction for the regions defined by the face or house localising contrasts. Given that numerous previous studies have found reduced responses to stimuli repeated after a short lag (repetition suppression) – in fusiform cortex, when attending to faces (e.g., Eger et al., 2005), and in parahippocampal cortex, when attending to houses (e.g., Yi and Chun, 2005) – further one-tailed t-tests for repeat minus control trials were performed on the attended–attended condition for faces and on the attended–attended condition for houses (collapsing across the factors hemifield and contralateral relation). As predicted, regions in left and right fusiform showed repetition suppression for faces that survived correction for the face localising contrast (no regions survived correction for the house localising contrast), and regions in parahippocampal/lingual cortices showed repetition suppression for houses that survived correction for the house localising contrast (no regions survived correction for the face localising contrast); see Table 3 and Fig. 4. Corresponding one-tailed t-tests on the three remaining conditions (attended–ignored, ignored–attended and

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[1] Note that the main effect of attended hemifield was not estimated efficiently (by design), given that the block repetition period of $2 \times (71 \, s + 15 \, s) \sim = 170 \, s$ means that any difference in signal is likely to be confounded by low-frequency noise and attenuated considerably by the consequent use of a high-pass filter cut-off of 128 s.

[2] Note that, though the selection of regions biases any interaction between region and stimulus category, it does not bias interactions involving hemifield or contralateral stimulus-relation.

[3] This appeared to be driven mainly by the different condition, i.e., when a house was in the ignored left hemifield, though the two-way interaction did not reach significance, $F(1,17)=2.69$, $p=0.12$.
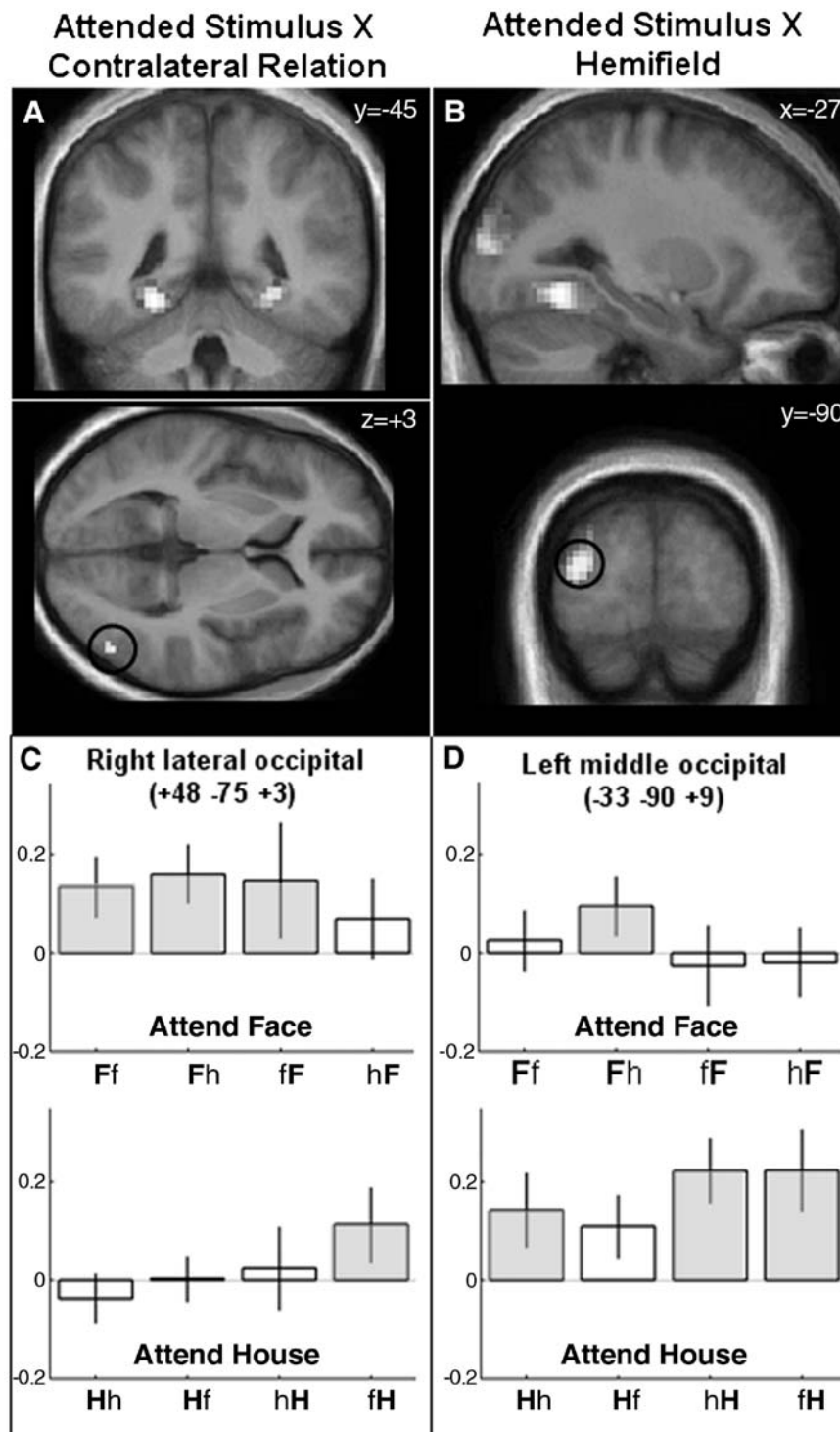
Fig. 2. Whole-brain analysis of the attended stimulus. Regions showing (A) interaction between attended stimulus category (face/house) and contralateral stimulus-relation (same/different) in parahippocampal regions within the house localising contrast (upper section) and in a right lateral occipital region within the face localising contrast (lower section), and (B) interaction between attended stimulus category and hemifield (left/right) in left parahippocampal and left middle occipital regions within the house localising contrast. Interaction effect is thresholded at $p < 0.01$ uncorrected, for purposes of illustration (localising contrast thresholded at $p < 0.001$ uncorrected), and displayed on a normalised T1-weighted image averaged across subjects. Panels (C) and (D) show plots of % signal change relative to the mean across voxels and scans for the 8 conditions of interest from the right and left occipital regions respectively (circled in A and B). Error bars show the 95% confidence interval. The condition label 'Ff' indicates an attended face on the left and an ignored face on the right; the condition label 'fH' indicates an ignored face on the left and an attended house on the right, etc. Grey fill illustrates the main pattern, i.e., greater activity when the preferred stimulus is in the contralateral hemifield, regardless of whether it is ignored or attended.

ignored–ignored) showed no such reliable effects (nor did contrasts testing for repetition-related increases in any condition).

Analysis of repetition effects: fROI analysis

As a final independent analysis, the data from the four maxima from the face and house localising contrasts (as above) were entered into an ANOVA on repetition effects with factors region (FFA vs. PPA), hemisphere, stimulus category, initial condition and repeat condition. The only reliable effects were the interaction between region and stimulus category, $F(1,17)=7.38$, $p<0.05$, with greater relative repetition suppression for faces in the FFA and for houses in the PPA, and the interaction between hemisphere and stimulus category, $F(1,17)=6.11$, $p<0.05$, with greater relative repetition suppression for faces in the right hemisphere and for houses in the left hemisphere. The repetition effects are shown for each region, stimulus category and repetition condition in Figs. 5A–H (error bars show 95% confidence intervals). The only four condition/region combinations to show reliable ($p<0.05$) repetition effects were in the attended–attended condition, and only for the stimulus category that the region preferred.

Nonetheless, the mean repetition suppression effect was as large for the attended–attended condition as for some of the other conditions (at least in the left and right FFA; Figs. 5A and B), differing only in the error associated with that mean. Following the suggestion of a reviewer, we performed post hoc contrasts of the repetition effect in the attended–attended condition against the mean repetition effect across the remaining three conditions. This contrast corresponds to the prediction that attention is necessary on both first and second presentations in order to observe repetition suppression. Repetition suppression was indeed reliably greater when houses were attended on both first and second presentations, for both left and right PPA, $t(18)=2.45$, $p<0.05$ and $t(18)=2.17$, $p<0.05$ respectively. For faces, there was a similar trend, but it did not reach significance in either left or right FFA, $t(18)=1.05$, $p=.15$ and $t(18)=1.06$, $p=.15$ respectively. Again, a similar pattern of results was found when the FFA and PPA were defined on an individual basis, though in this case, the pattern of repetition effects in the FFA was less clear (see Supplementary data).

Finally, we examined the repetition effects averaging across the four fROIs according to the preferred vs. non-preferred category for each fROI. If the categorical processing of ignored stimuli that was observed in the earlier analysis of the attended stimulus were sufficient to produce subsequent repetition effects, this would be the most sensitive test yet. For preferred stimuli, repetition suppression was highly reliable for the attended–attended condition ($p<0.001$), but did not reach significance for the other three conditions (Fig. 5I).[4] Indeed, the post hoc contrast of the attended–attended condition against the other three showed greater repetition suppression in the former, $t(18)=2.50$, $p<0.05$. For non-preferred stimuli, repetition suppression was not reliable in any condition (Fig. 5J).

Discussion

The first main finding of the present study is that neural repetition effects were only found to be reliable when both the first and second presentation of a stimulus were attended. Moreover, these repetition effects were "category-specific", in the sense that

they were only found in brain regions that expressed a preference for the stimulus category in question: i.e., in fusiform cortex (FFA) for faces and parahippocampal cortex (PPA) for houses. This was true for both the whole-brain and the functional region of interest (fROI) analyses. This conclusion is tempered by the fact that in neither analysis did the interaction between attention to first presentation and attention to second presentation reach significance. Nonetheless, the pattern of significant repetition effects was striking (Fig. 5): in the fROI analyses, the only four cases to show significant repetition-related reductions (repetition suppression) were the attended–attended conditions in left and right FFA for faces and left and right PPA for houses; none of the remaining 28 repetition effects across conditions/regions was significant. Moreover, when collapsing across fROI, there was evidence of greater repetition suppression when preferred stimuli were attended on both first and second presentations than when (on average) they were ignored on one or both occasions.

The second main finding concerns evidence for some processing of ignored stimuli; at least, of their category. The FFA and PPA showed greater responses to an ignored stimulus when it was from their preferred category than when it was from the non-preferred category. Nonetheless, the extent or the nature of this processing appears insufficient to produce subsequent repetition effects. We start by discussing this second finding of evidence for processing of ignored stimuli, before returning to the question of repetition effects.

Processing of ignored stimuli

Though selective attention to stimuli has long been known to modulate neural responses, the extent of the processing of ignored stimuli is still debated. For example, though reduced firing rates have been observed for a task-irrelevant stimulus when it co-occurs with an attended stimulus within the receptive field of neurones in V4 and IT cortex of nonhuman primates, this attenuation decreases as the distance from the attended stimulus increases (Moran and Desimone, 1985). Some functional imaging studies in humans have reported evidence for processing of "ignored" stimuli, particularly when they are aversive (Vuilleumier et al., 2001), whereas others have failed to find such evidence, provided that the attentional "load" is high enough (Pessoa et al., 2002; Rees et al., 1999), and the load reflects perceptual processing rather than central processing (Yi et al., 2004).

In the present study, we found both behavioural and neural evidence for processing of stimuli in the ignored hemifield. Reaction times were faster when the ignored stimulus was of the same category as the attended stimulus, resembling the so-called "bilateral redundancy gain" (Mohr and Pulvermuller, 2002). A similar effect was seen in the neural responses. In the fROI analyses for example, the PPA responses were greater when two houses were presented than when an attended house was accompanied by an ignored face. Furthermore, the greater PPA response for ignored houses than ignored faces was found even when the attended stimulus was a face (Fig. 3). Thus the PPA seemed to respond to its preferred stimulus in

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[4] If the size of repetition suppression in these three conditions were equal to that for the attended–attended condition, then the power for these one-tailed *t*-tests (with $N=18$ and alpha=.05) is 84%, 81% and 73% respectively.

[5] One potentially interesting complication of this story is that the PPA, but not FFA, tended to show a deactivation relative to baseline (i.e., relative to the control trials of blank ovals) when both the attended and ignored stimuli were of the non-preferred category, rather than an activation relative to baseline when the ignored stimulus was from the preferred category. In other words, when the attended stimulus was a face, the effect of a house in the ignored hemifield may be a disinhibition of the response in the PPA.
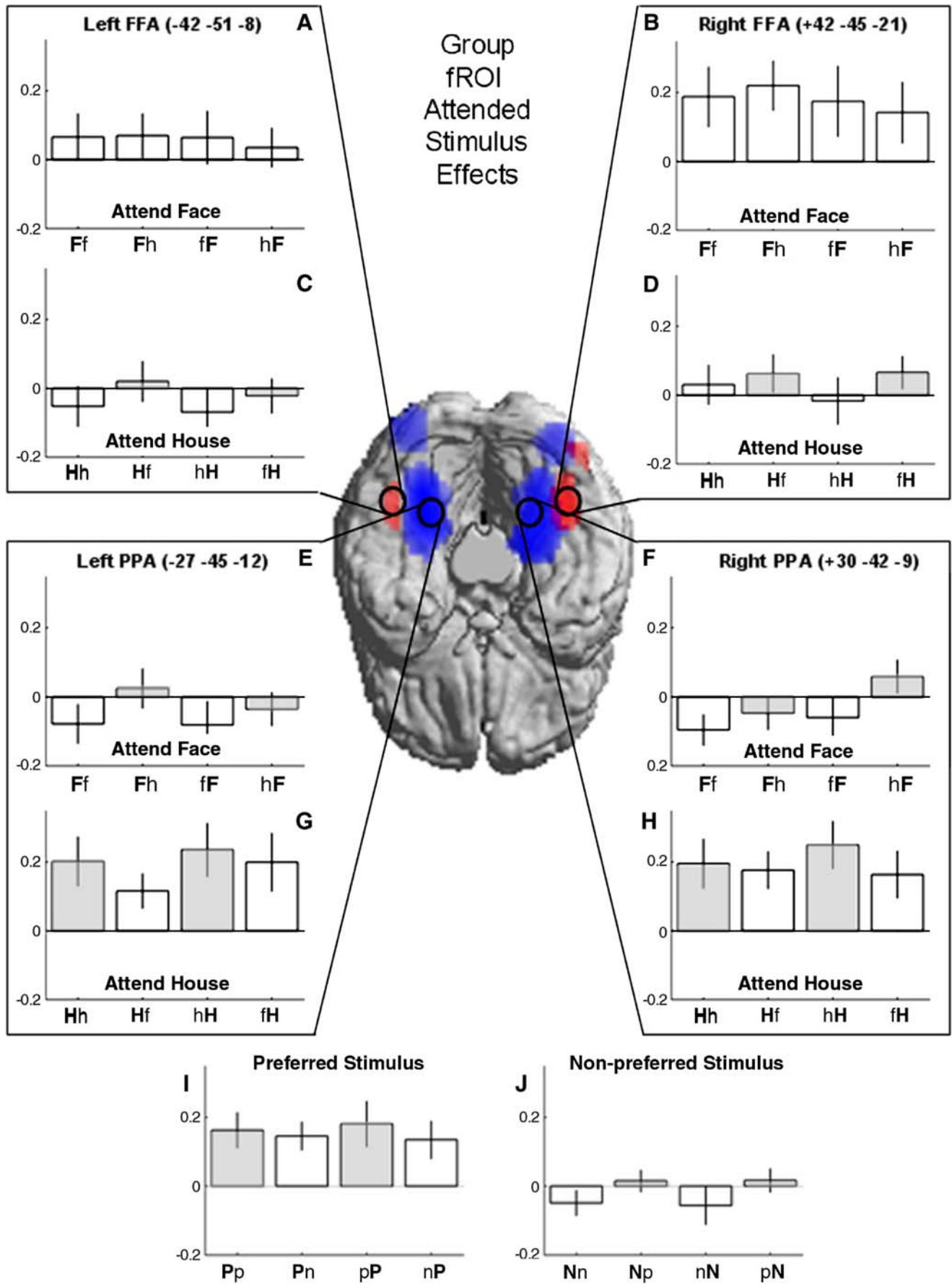
Table 3
Analysis of critical stimulus: voxels showing repetition suppression for stimuli attended on both first and second presentation, *t*-tests

Region	Voxels	MNI coordinates			Z
Faces					
Left midfusiform	3	−39	−48	−15	2.88*
Right midfusiform	28	+42	−42	−18	3.30[F]
Houses					
Left lingual	13	−33	−66	+3	4.68[H]
Right parahippocampus	74	+21	−51	−12	3.79[H]

[F]$p < 0.05$ SVC for face localising contrast (*$p = 0.06$ SVC). [H]SVC for house localising contrast.

the ignored hemifield, regardless of the stimulus category in the attended hemifield. An analogous, though less consistent, effect was seen in the FFA (see Supplementary data).[5] In the whole-brain analyses, similar evidence of responsiveness to the category of ignored stimuli was also seen in a right occipital face area and in a left occipital house area, though in these cases, there was an additional effect of hemifield, with greater responses to ignored stimuli from the preferred than non-preferred category only when ignored stimuli were in the contralateral hemifield (Fig. 2).

Of course, selective attention is a continuum rather than a dichotomy. Thus, the present behavioural and neural evidence for processing of stimuli in the ignored hemifield could reflect residual attentional resources; i.e., experimental conditions that were not of sufficiently high perceptual load (Lavie, 1995; Yi et al., 2004). This could include a small number of trials in which spatial attention was erroneously allocated to (or even eye movements made to) the side opposite to that instructed, or trials in which attention was captured by the task-irrelevant stimulus. While we cannot rule this out, we note that this would need to occur despite near-ceiling accuracy in the categorisation task. More important however is the fact that, even if the perceptual load was not high enough to abolish all processing of task-irrelevant stimuli, it was sufficient to prevent any detectable repetition effects for such stimuli.

Repetition effects

Some have claimed that behavioural effects associated with repetition, such as positive and negative priming, can occur outside attention (e.g., Jacoby et al., 1989; Szymanski and MacLeod, 1996; Tipper, 1985). In the case of positive priming, this has often been contrasted with the strong dependence of conscious memory on attention and used to support a distinction between implicit and explicit forms of memory (Parkin et al., 1990). However, other data suggest that both implicit and explicit memory depend on the level of attention (e.g., Crabb and Dark, 2003; Mulligan and Hornstein, 2000; Stone et al., 2000; and even though the dependence may be smaller for implicit memory, this can be explained by the measurement noise associated with the different types of tests used; Berry et al., 2006).

Note also that, while repetition effects have been reported for stimuli for which participants appear unaware, using masked priming paradigms (e.g., Dehaene et al., 2001), these are situations in which the initial presentation (the prime) is at an attended location in space and time (but simply presented too briefly for evidence of conscious registration). Indeed, if attention is reduced by unpredictable temporal occurrence of the prime, behavioural priming is no longer found in such paradigms (Naccache et al., 2002).

Here, we only found reliable neural repetition effects when both initial and repeated presentations were attended. This is consistent with some previous studies of Eger et al. (2004), Yi and Chun (2005), Yi et al. (2006) and Thoma and Henson (in press), but less consistent with others (Bentley et al., 2003; Murray and Wojciulik, 2004; Vuilleumier et al., 2005). There is no obvious difference in these two groups of studies in whether they used (1) spatial-based or object-based (or feature-based) attention, (2) faces, houses or objects, (3) short or long lags between repetitions. One reason for the discrepancy may again relate to the "strength" of the attentional manipulation, e.g., the perceptual load (Lavie, 1995). For example, the study of Murray and Wojciulik (2004), in which participants attended to either the fixation point (to detect a colour change) or the surrounding object, would seem to represent a relatively weak manipulation of attention (which was not a problem per se since this study had other aims). Therefore, their evidence for reliable (though reduced) repetition suppression for same versus different orientations may reflect relatively lower perceptual load than in the present study.

Whether the same perceptual load account applies to the Bentley et al. (2003) study, which is most similar to the present study in terms of spatial attention, intermediate lags and its use of faces, is less clear. In that study, four stimuli were presented around fixation, and participants performed a matching task on either the pair of stimuli above and below fixation, or the pair left and right of fixation. It is conceivable that this vertical versus horizontal manipulation of spatial attention, or the slightly longer presentation times (250 ms), did not entail perceptual loads as high as the present study, though this vertical/horizontal matching paradigm has been claimed to produce no awareness of identity, gender or expression of ignored faces (Vuilleumier et al., 2001). More noteworthy is that the lateral occipital region claimed to show repetition suppression for ignored faces in the Bentley et al. study was identified by a conjunction analysis of their attended–attended and ignored–ignored conditions, which does not imply that the effects would have been reliably identified for the ignored–ignored condition alone (see Nichols et al., 2005).

In the Vuilleumier et al. (2005) study, participants saw two overlapping line-drawings of objects in different colours and were instructed to attend to the object in one colour. When presented singularly at a later stage, repetition suppression was found for previously ignored objects in anterior fusiform regions (as well as repetition-related increases in lingual gyri). A perceptual load account would seem to have difficulty explaining these repetition effects, given that participants showed no evidence of explicit

Fig. 3. Group-defined functional region of interest (fROI) analyses of the attended stimulus. Responses are shown in four brain regions, left and right fusiform face area (FFA) and parahippocampal place area (PPA), whose coordinates are determined from the maxima of the main effect of attended faces vs. attended houses. Suprathreshold voxels for this localising contrast are rendered in red (faces>houses) and blue (houses>faces) on the ventral temporal surface of a canonical brain ($p < 0.001$ uncorrected, 10 contiguous voxels); FFA and PPA maxima are circled in black. Plots show % signal change relative to the mean across voxels and scans for the 8 conditions of interest. Error bars show the 95% confidence interval. Plots at the bottom (I, J) show data collapsed across fROI as a function of the stimulus category preferred by each fROI. The condition label 'Ff' indicates an attended face on the left and an ignored face on the right; the condition label 'fH' indicates an ignored face on the left and an attended house on the right, etc. Grey fill illustrates the main pattern of greater activity when the preferred stimulus is in the attended or ignored hemifield.
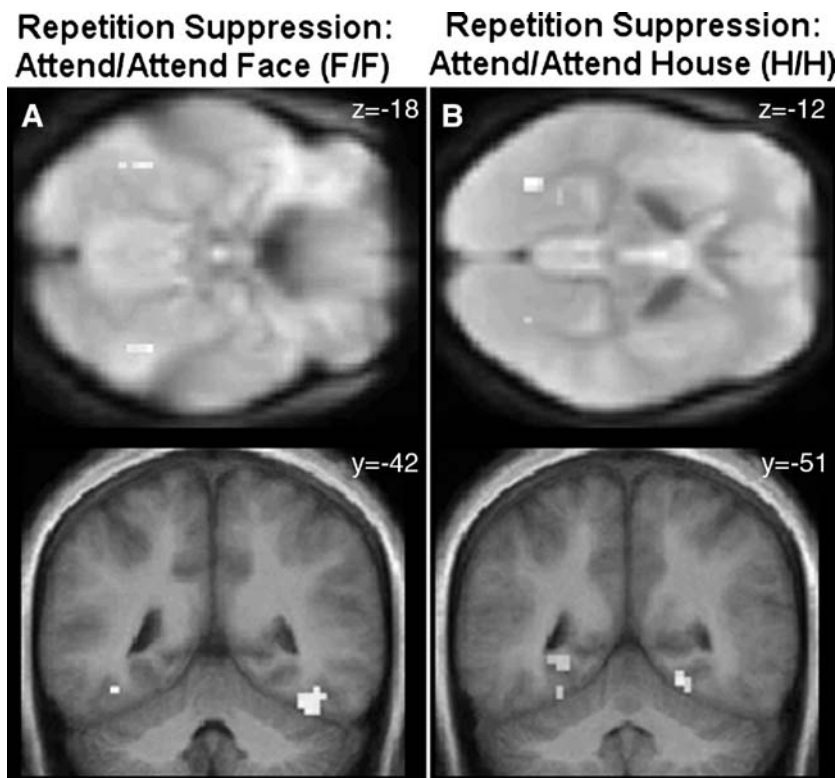
Fig. 4. Whole-brain analysis of repetition effects (critical stimulus). Regions showing reduced responses to repeated stimuli (repetition suppression) for (A) faces attended on both initial and repeat presentations, and (B) houses attended on both initial and repeat presentations. Repetition suppression effect is thresholded at $p < 0.01$ uncorrected for purposes of illustration (localising contrast thresholded at $p < 0.001$ uncorrected) and displayed on a transverse slice through the normalised EPI averaged across subjects (upper section) and on a coronal slice through the normalised T1-weighted image averaged across subjects (lower section).

memory for stimuli ignored on their initial presentation. Nonetheless, explicit memory was tested after a considerable delay, and it remains possible that the attentional selection of objects based on a feature (e.g., colour) is a less "effective" manipulation of attention than the current spatial manipulation.

Whatever the reasons for the apparent discrepancies across studies, the more important point is that, even if the present manipulation of spatial attention was "stronger" than in some previous studies, it was not strong enough to prevent any detectable processing of ignored stimuli. This suggests that the nature or extent of this processing is insufficient to induce whatever plasticity is required to produce repetition suppression when that stimulus is repeated several trials later.

Potential caveats

In the present design, the first and second presentations of stimuli in the attended–ignored and ignored–attended conditions necessarily occurred in different hemifields, unlike in the attended–attended

and ignored–ignored conditions. Thus the lack of repetition suppression in the attended–ignored and ignored–attended conditions could arise if repetition effects only occurred for stimuli repeated within the same hemifield. However, this cannot be a sufficient explanation because no repetition suppression was found for within-hemifield repetition in the ignored–ignored condition. Furthermore, in a separate experiment (Mouchlianitis and Henson, in prep), repetitions of houses in unilateral displays did not show evidence of greater repetition suppression for repetitions within versus between hemifields.

One must be cautious in comparing repetition effects across conditions in which the size of the response to the initial presentation differs. This is because a simple gain model, in which the difference between initial and repeated presentations is proportional to the response to the initial presentation, predicts smaller repetition suppression for weaker initial responses. In principle, this smaller effect size could explain our failure to observe reliable repetition suppression for stimuli that are not preferred by the region of interest (e.g., for faces in house-responsive regions; though see Avidan et al.,

Fig. 5. Group-defined functional region of interest (fROI) analyses of repetition effects (critical stimulus). Responses are shown in four brain regions, left and right fusiform face area (FFA) and parahippocampal place area (PPA), whose coordinates are determined from the maxima of the main effect of attended faces vs. attended houses. Suprathreshold voxels for this localising contrast are rendered in red (faces>houses) and blue (houses>faces) on the ventral temporal surface of a canonical brain ($p < 0.001$ uncorrected, 10 contiguous voxels); FFA and PPA maxima are circled in black. Plots show % signal change for repeat minus control trials across the 8 conditions of interest (collapsing across hemifield and contralateral relation). Error bars show the 95% confidence interval. Plots at the bottom (I, J) show data collapsed across fROI as a function of the stimulus category preferred by each fROI. The condition label 'F/F' indicates a face attended on both initial and repeat presentations; the condition label 'h/H' indicates a house ignored on its initial presentation but attended on its repeat presentation, etc. Grey fill illustrates the pattern of repetition suppression only for stimuli preferred by the given region, and that were attended on both initial and repeat presentations.
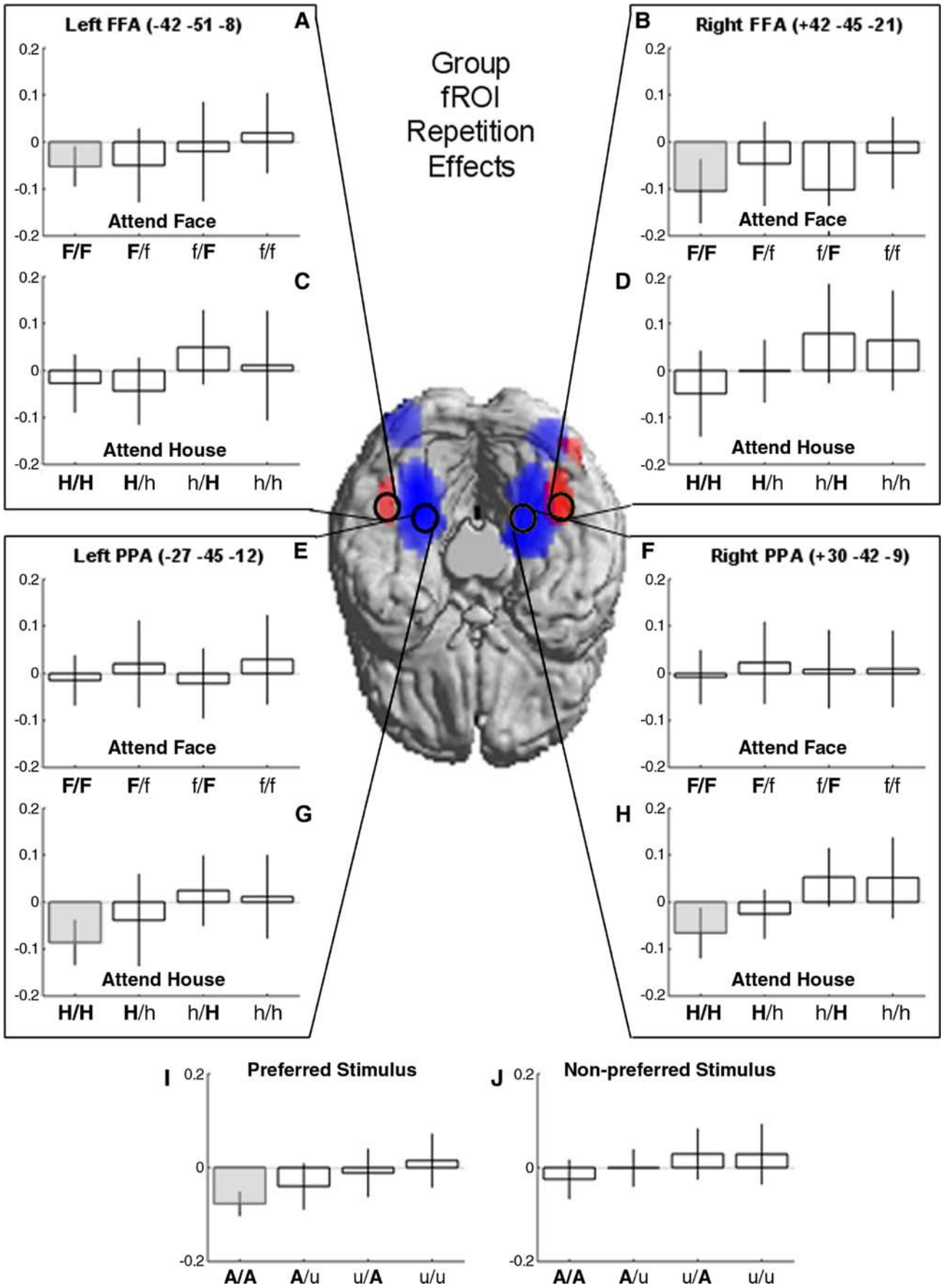
2002). It could also explain our failure to find repetition suppression in the ignored–attended and ignored–ignored conditions, given the weaker response to the initial presentation in these conditions relative to conditions in which the initial presentation was attended. Its ability to explain our failure to find repetition suppression in the attended–ignored condition is less clear, though it is possible that the smaller "dynamic range" for ignored stimuli also makes any repetition effects more difficult to detect (on second presentations). While we cannot rule out these possibilities in the present study, we note that several previous studies (Harris and Nakayama, 2007; Murray and Wojciulik, 2004; Yi and Chun, 2005; Yi et al., 2006) have provided evidence that modulations of repetition suppression cannot be explained by such simple gain mechanisms.

Laterality effects

We are not aware of any previous fMRI studies that have investigated effects of visual hemifield on responses to faces and houses. In our data, any effects of attended hemifield in FFA did not reach significance. This might be regarded as surprising, given evidence for superior processing of faces in the left than right visual field, though we note that such visual field effects are sensitive to precise conditions (Sergent, 1985). Having said this, there were clear effects of hemisphere, with greater overall responses to faces in the right FFA than left FFA (which may still reflect a right hemisphere specialisation for face processing, even if such lateralisation is unaffected by which hemifield is attended when using bilateral displays).

There were effects of attended hemifield in PPA (consistent perhaps with the suggestion that PPA codes object representations that are more sensitive to visual information in the periphery than does FFA, Levy et al., 2001). Hemifield effects were also found in more posterior regions, namely the right occipital region that showed a preference for faces and a left occipital region that showed a preference for houses. In all these cases, the hemifield effects reflected stronger responses to preferred stimuli in the ignored hemifield when that hemifield was contralateral relative to ipsilateral.

Conclusions

The purpose of the present study is not to claim that the effect of attention on neural plasticity is all-or-none – a better conclusion is clearly that neural plasticity is modulated by the level of selective attention – rather its purpose is to counter claims that repetition effects are unaffected by attention, or can occur in the absence of attention (e.g., under conditions of high perceptual load). Under the present conditions, diversion of spatial attention away from either the initial or the repeated presentation of a visual image did not result in detectable repetition suppression for that image, despite evidence for some processing of the image in such cases, and despite detectable repetition effects when it was attended on both presentations.

Acknowledgments

Appendix A. Supplementary data

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Supplementary Material

Individually-defined fROIs

Following a request from a reviewer, the data were also analysed by defining fROIs on an individual basis, rather than on a group basis (as in the main paper). Defining fROIs individually is a more common practice for the FFA and PPA, and allows for possible anatomical variability across participants in the functional organisation of their brains (see, e.g., Saxe, Brett, & Kanwisher, 2006, for further discussion). Therefore, each participant's SPM for the same localising contrast (attend faces vs. attend houses, and vice versa) was thresholded at p<.001 uncorrected, and the coordinates of the maximum within left and right fusiform or parahippocampal cortices recorded.[1] At this threshold, the fROIs were identified in most, though not all, participants. The number of such participants, and the mean and range of their MNI coordinates, are shown in Table S1.

The response of each of these 4 fROIs across the 8 conditions in the analyses of the Attended Stimulus and of the Repetition Effects are shown in Figure S1 and S2 respectively (cf. Figures 3 and 5 in the main paper). In general, these individually-defined results are similar to the group-defined results, though there are a few notable differences. Firstly, the overall signal change in the analysis of the Attended Stimulus was greater, particularly for the FFA (Figure S1). This is probably because voxels with larger signal changes are more likely to be selected (i.e, more reliable in the localising contrast for individual participants), and hence the mean signal change across participants is likely to be greater than when this latitude is removed by matching voxels across participants in the group-analysis. Secondly, in the analysis of Repetition Effects (Figure S2), there was no longer reliable repetition suppression for faces in the attended-attended condition in the left FFA, and now repetition

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[1] Note that the functional images were still spatially normalised to Talairach space, as in the main paper, and that the data from these maximal voxels reflect a weighted average of nearby voxel values, given the spatial smoothing employed. Note also that our functionally-defined regions were identified by an orthogonal contrast within the same experimental session (i.e, for the same stimuli under the same task), which avoids the problems associated with using separate "localiser" sessions (Friston et al., 2006).

suppression for faces in the attended-attended condition in the right PPA reached significance. Finally, the post hoc contrasts of repetition suppression in the attended-attended condition against the mean repetition suppression effect across the remaining three conditions (see main paper) was again reliable when houses were attended on both first and second presentations, for both left and right PPA, t(17) = 2.58, p<.05 and t(16)=2.07, p<.05 respectively. For faces however, there was no such evidence in either left or right FFA, t(12)=-1.35 and t(15)=0.004 respectively.

In order to perform repeated-measures ANOVAs analogous to those in the main paper, the data were restricted to the 11 participants in which all four fROIs could be identified.

Analysis of Attended Stimulus: fROI analysis

As in group-based fROI analyses, the ANOVA with factors region (FFA vs. PPA), hemisphere (left vs. right), stimulus-category, attended hemifield and contralateral stimulus-relation showed a reliable five-way interaction, F(1,10)=11.6, p<.01. When decomposing this interaction into separate ANOVAs for attended faces and attended houses, there were reliable four-way interaction between region, hemisphere, attended hemifield and contralateral stimulus-relation in both cases, F(1,10)=5.06, p<.05, and F(1,10)=9.20, p<.05, respectively, also as in the main paper.

For attended faces, the subsequent three-way ANOVAs on FFA and PPA separately showed only a reliable main effect of contralateral stimulus-relation, F(1,10)=7.81, p<.05. This effect, of greater responses when the contralateral (ignored) stimulus-category was also a face (see Figure S1A&B), did not reach significance in the group-based analysis of the FFA, though matches the general pattern seen in the PPA. For the PPA, there was a reliable three-way interaction between hemisphere, attended hemifield and contralateral stimulus-relation, F(1,10)=11.7, p<.01. Follow-on analyses on left and right PPA separately showed only a main effect of contralateral stimulus-relation in both cases, F(1,10)>47.3, p<.001, as in the group-based analyses, plus an interaction between attended hemifield and contralateral stimulus-relation in the right PPA, F(1,10)=7.5, p<.05. The main effects of

contralateral stimulus-relation reflected greater responses when the contralateral (ignored) stimulus-category was different, i.e, a house (see Figure S1E&F). The interaction with hemifield in right PPA reflected greater responses to attended faces in the right hemifield.

For attended houses, the subsequent three-way ANOVAs on FFA and PPA separately showed a reliable main effect of contralateral stimulus-relation in both regions, $F(1,10)=17.0$, $p<.005$, and $F(1,10)=6.96$, $p<.01$, respectively. In all cases, responses were greater when the contralateral (ignored) stimulus-category corresponded to the preferred stimulus for that region (Figure S1C&D, G&H), as also found in the group-based fROI analyses. For the PPA, there was an additional two-way interaction between hemisphere and attended hemifield, $F(1,10)=9.99$, $p<.05$, reflecting greater responses when the attended stimulus was in the contralateral hemifield.

In summary, these results support the general results from the group-based fROI analyses in the main paper, with evidence of category-specific processing of stimuli in the ignored hemifield.

Analysis of Repetition Effects: fROI analysis

The data from the individually-defined fROI were also entered into an ANOVA on repetition effects with factors region (FFA vs. PPA), hemisphere, stimulus-category, initial condition and repeat condition. As for the group-based analyses, the was a reliable interaction between region and stimulus-category, $F(1,10)=5.22$, $p<.05$, with greater relative repetition suppression for faces in the FFA and for houses in the PPA. Unlike the group-based analyses, there was also an interaction between region and initial condition, $F(1,10)=5.95$, $p<.05$, with a greater effect of initial attention in the PPA than in the FFA. There was also a reliable four-way interaction between hemisphere, stimulus-category, initial condition and repeat condition, $F(1,10)=6.42$, $p<.05$. This was followed-up with separate ANOVAs for faces and houses. When faces were the critical stimulus, the only reliable effect was the two-way interaction between hemisphere and initial condition, $F(1,10)=5.16$,

p<.05, which reflected greater effects of attention to first presentations in the right than left hemisphere. When houses were the critical stimulus, there were no reliable effects. Given that these latter two effects were not found in the group-based analyses, they are not interpreted further.

Summary

In general, the results from the individually-defined fROIs are not as clear cut as in the group-defined fROIs. This may reflect the practical difficulty in identifying the FFA or PPA in some participants. Though maxima within the fusiform or parahippocampal cortices might have been identified for all participants by lowering the statistical threshold, this causes ambiguity for other participants in which multiple such maxima emerge. Moreover, although lowering the threshold might restore the statistical power to that of the group-defined analyses, it may also introduce more random noise into the data. Alternatively, the anatomical variability in the location of the FFA and PPA may not, in fact, be large relative to the spatial smoothness of the present data, in which case the group-defined fROIs will be more sensitive. Whatever the reason for the differences in the group-defined and individually-defined fROI analyses, the general conclusions of the main paper would not appear to be disputed.

Behavioural Data

The RTs for the analysis of the Attended Stimulus and for the Repetition Effects in analysis of the Critical Stimulus, are shown in Tables S2 and S3 respectively.

Table S1. Individually-defined fROIs. n = Number of participants in which at least
one voxel within fusiform or parahippocampal cortex survived p<.001 uncorrected in
the localising contrast of faces vs. houses. Mean, Min and Max give idea of central
tendency and range across participants of the MNI coordinates for the maxima of
these contrasts.

	Left FFA	Right FFA	Left PPA	Right PPA
n	12	15	17	16
Mean	-39 -48 -18	+39 -50 -19	-25 -48 -13	+28 -44 -11
Min	-48 -63 -24	+33 -66 -24	-33 -60 -21	+18 -51 -21
Max	-30 -36 -12	+45 -33 -12	-21 -39 -6	+36 -39 -6

Table S2. Mean (M) and Standard Error of Mean (SEM) for Reaction Times (ms) as a function of condition in the analysis of the Attended Stimulus. The condition label '**F**f' indicates an attended face on the left and an ignored face on the right; the condition label 'f**H**' indicates an ignored face on the left and an attended house on the right, etc.

	Ff	**F**h	f**F**	h**F**	**H**h	**H**f	h**H**	f**H**
M	561	581	561	564	594	593	584	585
SEM	36	40	38	38	43	42	37	37

Table S3. Mean (M) and Standard Error of Mean (SEM) for Repetition Effects (control minus repeat trials) in Reaction Times (ms) as a function of condition in the analysis of the Critical Stimulus. The condition label '**F/F**' indicates a face attended on both initial and repeat presentations; the condition label 'h/**H**' indicates a house ignored on its initial presentation but attended on its repeat presentation, etc.

	F/F	**F/**f	f/**F**	f/f	**H/H**	**H/**h	h/**H**	h/h
M	4	3	-10	12	-13	-2	11	-3
SEM	9	13	7	6	7	11	8	8

Figure S1. Individually-defined Functional Region-of-Interest (fROI) analyses of the attended stimulus (cf. Figure 3 in main paper). Responses are shown in four brain regions, left and right fusiform face area (FFA) and parahippocampal place area (PPA), whose coordinates are determined from the maxima of the main effect of attended faces vs. attended houses for each participant separately. Plots show % signal change relative to the mean across voxels and scans for the 8 conditions of interest. Error bars show 95% confidence intervals. The condition label '**F**f' indicates an attended face on the left and an ignored face on the right; the condition label 'f**H**' indicates an ignored face on the left and an attended house on the right, etc. Grey fill illustrates the main pattern of greater activity when the preferred stimulus is in the ignored hemifield.

Figure S2. Individually-defined Functional Region-of-Interest (fROI) analyses of repetition effects (critical stimulus; cf. Figure 5 in main paper). Responses are shown in four brain regions, left and right fusiform face area (FFA) and parahippocampal place area (PPA), whose coordinates are determined from the maxima of the main effect of attended faces vs. attended houses for each participant separately. Plots show % signal change for repeat minus initial presentations across the 8 conditions of interest (collapsing across hemifield and contralateral relation). Error bars show 95% confidence intervals. The condition label '**F/F**' indicates a face attended on both initial and repeat presentations; the condition label 'h/**H**' indicates a house ignored on its initial presentation but attended on its repeat presentation, etc. Grey fill illustrates reliable repetition suppression, which tends to be only for stimuli preferred by the given region and that were attended on both initial and repeat presentations.