

# Inter-relationships between attention, activation, fMR adaptation and long-term memory

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**fMR adaptation in the ventral visual pathway reflects information processing that may contribute to implicit and explicit memory. In experiments that employed <1 s repetition lag, we found that attention increases adaptation for repeated objects in brain regions at the top of the visual processing hierarchy (anterior fusiform and parahippocampal gyri) but that it can still appear with minimal attention in most of the fusiform bilaterally. Of the ventral visual regions showing adaptation, the parahippocampal region and LOC showed the strongest correlation between adaptation magnitude and recognition memory across subjects. Although there was some overlap, regions showing correlations between adaptation and priming lay more posteriorly within the fusiform region. The positive association between encoding-related activation and adaptation suggests that over an entire test set, memory performance can be determined by neural events occurring in the peristimulus period. This may reflect stronger engagement of attention at encoding.**

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## Introduction

Adaptation, also termed repetition suppression (Grill-Spector and Malach, 2001; Henson and Rugg, 2003), is thought to reflect stimulus specific perceptual memory and its magnitude has been used to index item resemblance (Grill-Spector and Malach, 2001; Grill-Spector, 2004) as well as memory strength (Epstein et al., 2005; Turk-Browne et al., 2006).

Along the ventral visual stream, repetition induced neural response attenuation has been shown to be greater when a stimulus is explicitly remembered (Turk-Browne et al., 2006). Interestingly, adaptation can also be found when behavioral differences between initial and repeat presentations are absent (Maccotta and Buckner, 2004; Klaver et al., 2007) and when test stimuli are not consciously

perceived (Dehaene et al., 2001). In addition, it has been observed at locations differing in functional specialization (Grill-Spector et al., 2006), suggesting that the neural mechanisms underlying adaptation vary according to experimental context and neuroanatomical locale (Schacter et al., 2007). For instance, it has been demonstrated for repeated contours in early visual areas (Kourtzi and Huberle, 2005), for repeated shapes in lateral occipital cortex (Murray and Wojciulik, 2004) and in the parahippocampal gyrus for repeated black and white scenes (Yi and Chun, 2005).

In this work, we clarify the relationships among attention, encoding-related activation, adaptation and long-term explicit memory (henceforth, the term ‘activation’ refers to ‘encoding-related activation’). Specifically, our goal was to evaluate how attention may modulate adaptation at various points along the ventral visual pathway noting that links between repetition effects and the prefrontal cortex are already well established (Dobbins et al., 2004; Maccotta and Buckner, 2004; Wig et al., 2005). We also sought to uncover where along this pathway adaptation and long-term explicit memory correlate best (Turk-Browne et al., 2006), thus differentiating the present work from the many adaptation studies of implicit memory/priming.

Attention during encoding strongly influences later memory performance (Mack and Rock, 1998). For example, paying attention to a stimulus benefits memory whereas dividing attention impairs performance on many measures of memory (Craig et al., 1996; Mulligan, 1998). The neural counterpart to this behavioral finding is that an attended stimulus is accompanied by relatively greater activation of the ventral visual cortex than an unattended stimulus (Brefczynski and DeYoe, 1999; Gandhi et al., 1999; Kastner and Ungerleider, 2000). Further, activation in stimulus specific cortex is relatively suppressed for ignored items (Gazzaley et al., 2005). Finally, across many studies, there is a strong and consistent relationship between activation magnitude at encoding in a number of brain regions and subsequent memory (Brewer et al., 1998; Wagner et al., 1998; Kirchoff et al., 2000).

The relationship between attention and adaptation is more complex. On the one hand, attention has been shown to be critical for adaptation (Eger et al., 2004; Murray and Wojciulik, 2004; Vuilleumier et al., 2005; Yi and Chun, 2005). On the other hand, stimulus repetition effects have also been observed without

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conscious awareness (Schott et al., 2005), suggesting that adaptation can be automatic (Wiggs and Martin, 1998), depending on the task and on where in the cortex one looks. Furthermore, the correlation between the magnitude of adaptation and memory appears to be task dependent, there being reports of both clear (Epstein et al., 2005; Turk-Browne et al., 2006) and absent (Maccotta and Buckner, 2004) correlations between adaptation within the ventral visual pathway and memory.

To reconcile some of the inconsistent past findings, we posit that a part of the adaptation response within the ventral visual pathway may arise from visual processing sensitive to perceptual repetition and may occur with minimal engagement of attention. This component would not be expected to contribute to the formation of an *explicitly remembered* percept, unlike the attention-sensitive component that contributes to explicit memory (see Slotnick and Schacter, 2004). A similar dissociation between ventral visual regions showing adaptation with and without accompanying behavioral priming has been recently uncovered (Ganel et al., 2006; Sayres and Grill-Spector, 2006).

Many recent experiments evaluating the importance of attention in adaptation used paradigms that require ignoring the stimulus that would otherwise generate adaptation (Eger et al., 2004; Murray and Wojciulik, 2004; Vuilleumier et al., 2005; Yi and Chun, 2005). These paradigms studied the impact of divided attention on adaptation using strong manipulations of attention, whereas the original descriptions of repetition suppression in primate work referred to experiments involving passive viewing, where attention was not necessarily engaged (Baylis and Rolls, 1987; Fahy et al., 1993; Li et al., 1993). The current work seeks to study the effect of attention somewhere in the middle of the continuum (Klaver et al., 2007) given that the manner in which attention is divided influences adaptation and memory (Chun and Turk-Browne, 2007).

Another related issue pertains to the link between memory and where adaptation is observed. Although many areas in the ventral visual cortex demonstrate adaptation, adaptation may be correlated with explicit memory only in a subset of these regions (Turk-Browne et al., 2006). Also, while behavioral priming and repetition suppression have been shown to occur at the same time, they may not be correlated (Maccotta and Buckner, 2004; McMahan and Olson, 2007). Here, we sought to show how adaptation in different regions might contribute to implicit and explicit memory.

Finally, behavioral (Bentin and Moscovitch, 1988), electrophysiological (Nagy and Rugg, 1989) and functional imaging (Henson et al., 2004) work suggests a distinction between short and long-lag repetition effects. In terms of pure repetition suppression magnitude, short lags between repeated and novel stimuli generate significantly larger effects than longer lags (Baylis and Rolls, 1987; McMahan and Olson, 2007). Given that the magnitude of adaptation with long-lag repetition in the PPA tracks long-term explicit memory (Turk-Browne et al., 2006), we would expect that short-lag (<1 s.) repetition effects should be as, if not more, predictive of such memories (Brozinsky et al., 2005). Short-lag repetition designs also serve to eliminate interference effects from intervening stimuli arising from semantic similarity (see Klaver et al., 2007). Highly emotional stimuli might also interfere with subsequent retrieval. An extreme example of this is how the interposition of emotional stimuli can disrupt the maintenance of visual memories (Dolcos and McCarthy, 2006).

## Materials and methods

### Experiment 1

This experiment comprised three conditions intended to evaluate the effect of attention on activation, adaptation and explicit memory (Fig. 1). In two of the conditions, ‘attend target’ conditions, we determined the magnitude of activation and adaptation to incidentally perceived objects, when volunteers were instructed to respond to a central target cross. Critically, although target detection was expected to engage vigilant attention, directing the volunteer away from object viewing, the suppression of incidental object processing was expected to be incomplete (cf. (Vuilleumier et al., 2005; Yi and Chun, 2005)). Adaptation magnitude was observed at two target frequencies. Target frequency is known to modulate demands on sustained attention (Sarter et al., 2001). Raising perceptual load in the primary task reduces the processing of incidentally processed stimuli (Lavie, 1995). This *generally* reduces ventral visual pathway activation to the incidentally processed stimulus but the specific experimental set-up can strongly influence the result (Rose et al., 2005).

We used two target frequencies because a priori we had no idea of which frequency might be more effective in attenuating adaptation. At both target frequencies, however, we predicted that adaptation would occur, but that the subsequent identification of the presented objects would be poor.

In a third, ‘attend objects’ condition intended to directly evaluate the effect of attention on memory and adaptation, volunteers viewed the same type of stimuli but were instructed to attend to the objects and to ignore the crosses. We expected this manipulation to enhance recognition memory for objects and to observe both greater activation as well as greater adaptation for these objects.

### Participants and procedure

Seventeen healthy right-handed volunteers (6 males, mean age 22 years, range 20–25 years) gave informed consent for this study.

An event-related fMRI design was used. Visual stimuli were presented in two concurrent streams (Fig. 1). In the ‘attend target’ part of the experiment, volunteers were instructed to attend to the stimulus stream comprising a red square, a blue square and a blue cross. The appearance of a central blue square cued the start of a target detection block. Periodically, a blue cross would appear for 250 ms. Volunteers were required to respond to the blue cross by pressing a button with their right index finger. Each of four experimental runs (444 s each) contained four task blocks. A target cross appeared every 3 s (Infrequent Targets; IT) in two blocks, and twice every 3 s (Frequent Targets; FT) in the remaining two blocks. The ‘attend target’ blocks (84 s) alternated with baseline periods (21 s) during which volunteers maintained fixation on a central red square. The central squares and the target crosses subtended a visual angle of  $0.57 \times 0.57^\circ$ .

The second concurrent stream of stimuli was interleaved with the first and comprised object quartets (Chee et al., 2006) presented at varying intervals. Quartets of stimuli were used to maximize adaptation effects as it is known that repetition suppression effects increase with greater repetition (Grill-Spector and Malach, 2001) up to about 8 items. Each of the four objects within a quartet appeared for 500 ms (stimulus duration; SD), with an inter-stimulus interval (ISI) of 250 ms. The interval between each

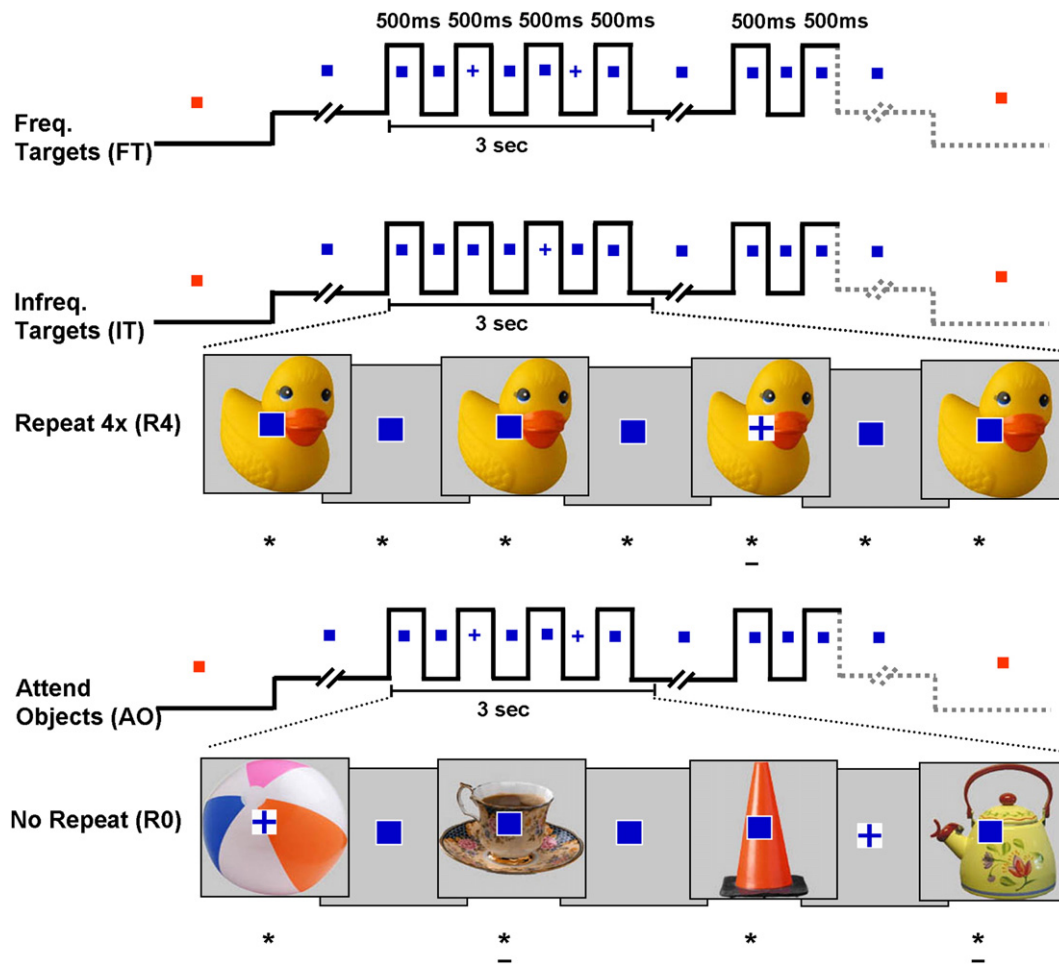


Fig. 1. Picture stimuli and presentation sequence of each of the three conditions (FT, IT and AO) appearing in Experiment 1. Object quartets were either repetitions of four identical objects (R4) or four different novel objects (R0). These two different types of quartets occurred in all three conditions. Each picture in a quartet appeared for a stimulus duration (SD) of 500 ms. The pictures were separated by an interval of 250 ms. Quartets were presented with a mean inter-quartet interval (IQI) of 8500 ms. In the ‘attend targets’ conditions (FT and IT), volunteers attended to the central blue square and responded when this changed to a blue cross. They were asked to ignore the pictures. In the ‘attend objects’ condition, volunteers attended to the pictures keeping their gaze in the centre of the image. They were to respond when they saw a household item. The asterisks (which did not appear in the experiment) under the stimuli indicate the stimuli that were to be attended to in the given condition. Underscored asterisks indicate stimuli that required a response. The appearance of a red square indicated a fixation period.

quartet could be 6, 9 and 12 s, with a mean interval of 8.5 s. Each quartet comprised either four different objects (no repeat; R0) or four instances of the same object (repeat 4×; R4). Six object quartets appeared in each block, giving a total of 360 full color inanimate objects. Half of these were household objects. All objects subtended a visual angle of approximately  $3.8 \times 3.8^\circ$ . The block and object quartet presentation order was randomized for each subject.

The ‘attend objects’ condition involved two additional runs. Subjects saw the same type of stimuli as in the FT version of the ‘attend targets’ task but were now expected to attend to the objects instead of the crosses and to press a button when they saw a household object. Equal numbers of household and non-household objects appeared in random order. At the end of the experiment, volunteers were given a surprise recognition memory test. The test items were chosen from the *first object* of each quartet. Recognition memory was evaluated using  $A'$ , a non-parametric measure of memory (Snodgrass and Corwin, 1988). The order in which this section was presented was counterbalanced across subjects.

#### Imaging protocol

Imaging was performed with a 3.0-T Allegra MR scanner (Siemens, Erlangen, Germany). Functional scans were acquired using a gradient-echo EPI sequence with TR of 3000 ms, FOV  $19.2 \times 19.2$  cm,  $64 \times 64$  matrix. Thirty-two oblique axial slices approximately parallel to the AC-PC line and 3 mm thick (0.3 mm gap) were obtained. High-resolution T1 anatomical images were also acquired. Stimuli were projected onto a screen at the back of the magnet. The participants viewed the screen via a mirror.

#### Data analysis

Functional images were processed using Brain Voyager QX version 1.79 (Brain Innovation, Maastricht, Holland). Image preprocessing included motion correction, slice-time correction, spatial normalization to Talairach space and spatial smoothing (8 mm full width at half-maximum Gaussian kernel) (Chee et al., 2006). Functional images were analyzed using a general linear model (GLM) with six event-related predictors (attend objects no repeat—AOR0, attend objects repeat 4×—AOR4, infrequent

targets no repeat—ITR0, infrequent targets repeat 4×—ITR4, frequent targets no repeat—FTR0, frequent targets repeat 4×—FTR4). Each predictor was convolved with a canonical hemodynamic response function (HRF) and its temporal derivative. Parameter estimates of activation were subjected to a mixed effects analysis with subjects as the random variable. We performed a voxel-by-voxel analysis of variance (ANOVA) to uncover the brain regions sensitive to differences in attention, repetition of objects and their interaction. The analysis was performed at a whole-brain level with a significance threshold of  $p < 0.001$  (uncorrected). The voxel cluster threshold was 5 functional voxels. Regions that showed a main effect of repetition and an interaction between attention and repetition were of interest.

Adaptation magnitude was evaluated within ROI by obtaining the difference in parameter estimates for events involving non-repeated and repeated object conditions (Yi and Chun, 2005). The contrasted pairs corresponded to each combination of attend-object and attend-target versions of the experiment; i.e. AOR0-AOR4, ITR0-ITR4 and FTR0-FTR4.

### Experiment 2

In the second experiment (Fig. 2), we determined the extent to which adaptation magnitude for attended objects correlates with individual differences in behavioral priming and recognition memory performance. We were also interested in determining the locations of regions showing these strong correlations.

Twenty healthy right-handed volunteers (10 males, mean age 21 years, range 20–27 years) gave informed consent for this study. The same object pictures used in Experiment 1 were used in this event-related fMRI experiment, except that the pictures appeared in pairs instead of quartets to reduce memory interference effects. There were no squares. Object pictures were separated by a fixation cross. Subjects were instructed to respond to a household object by pressing a button with their right index finger. Following the scan, subjects were given a surprise recognition memory test outside the scanner. They were tested only on the first object in a pair.

To establish objectively how adaptation might correlate with recognition memory across different individuals, we created a

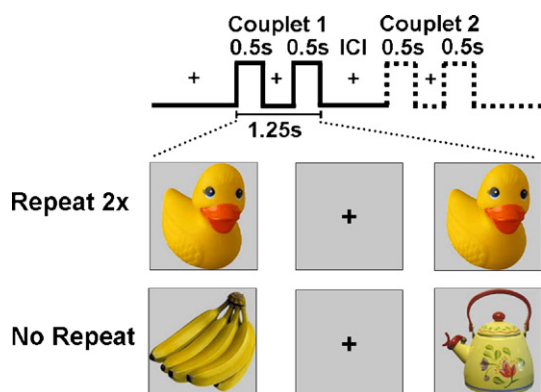


Fig. 2. Stimuli and presentation sequence used in Experiment 2. These objects were presented in pairs separated by a fixation cross. Subjects pressed a button if the presented object was a household object. Each picture was presented for a stimulus duration (SD) of 500 ms and was separated by 250 ms. Couplets appeared at a mean inter-couplet interval of 8500 ms.

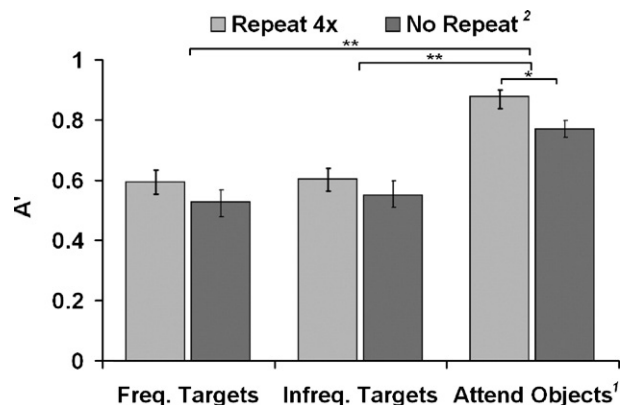


Fig. 3. Recognition performance measured by  $A'$  to repeated and non-repeated objects as a function of subsequent memory. Recognition performance was better in the 'attend object' condition than for the other two attend target conditions but was not different between the two target conditions (\*significant at  $p < 0.05$ , \*\*significant at  $p < 0.001$ ).

mask of all brain regions showing adaptation to all three conditions from Experiment 1 and constrained the correlation of adaptation to  $A'$  scores and priming benefits to these voxels. We used a threshold of  $p < 0.001$  (corrected) to create the mask. This ensured an unbiased selection of regions for a further correlation analysis. Regions showing correlations were those where  $r$  was significant at  $p < 0.05$ . This latter number is not the threshold for detecting voxels but is an indicator that the slope of the correlation is significantly different from zero.

## Results

### Experiment 1: behavioral results

Recognition data were available for 16 of the 17 subjects. Attention facilitated the recognition of objects as expressed by higher hit rates ( $A'$  for AO vs. FT vs. IT: 0.82 vs. 0.56 vs. 0.60;  $F(2,30)=95.01$ ,  $p < 0.001$ ; Fig. 3). There was also a significant interaction between attention and repetition ( $F(2,30)=11.21$ ,  $p < 0.001$ ). Repetition improved recognition for objects only when they were attended (AOR4 vs. AOR0:  $t(15)=7.78$ ,  $p < 0.001$ ; FTR4 vs. FTR0:  $t(15)=1.71$ ,  $p=0.11$ ; ITR4 vs. ITR0:  $t(15)=1.39$ ,  $p=0.19$ ). Recognition of unattended objects was only slightly above chance. The hit rates in the two attend target conditions did not differ significantly ( $t(15) < 1$ ).

### Experiment 1: imaging results

In a whole-brain analysis, adaptation was evident throughout the ventral visual pathway in all three conditions (Fig. 4a). It was maximal bilaterally in the parahippocampal and in the lateral occipital regions. Both encoding-related activation and adaptation were highest for the 'attend object' condition in the parahippocampal region (Talairach coordinates:  $-24, -40, -8$ ; encoding activation for AO vs. FT:  $t(16)=5.65$ ,  $p < 0.001$ ; AO vs. IT:  $t(16)=7.9$ ,  $p < 0.001$ ; FT vs. IT:  $t(16) < 1$ ; adaptation (R4 vs. R0) for AO:  $t(16)=6.49$ ,  $p < 0.001$ ; IT:  $t(16)=2.15$ ,  $p < 0.05$ ; FT:  $t(16)=4.32$ ,  $p < 0.001$ ).

There was greater activation within the ventral visual pathway and superior parietal regions in FT relative to IT condition



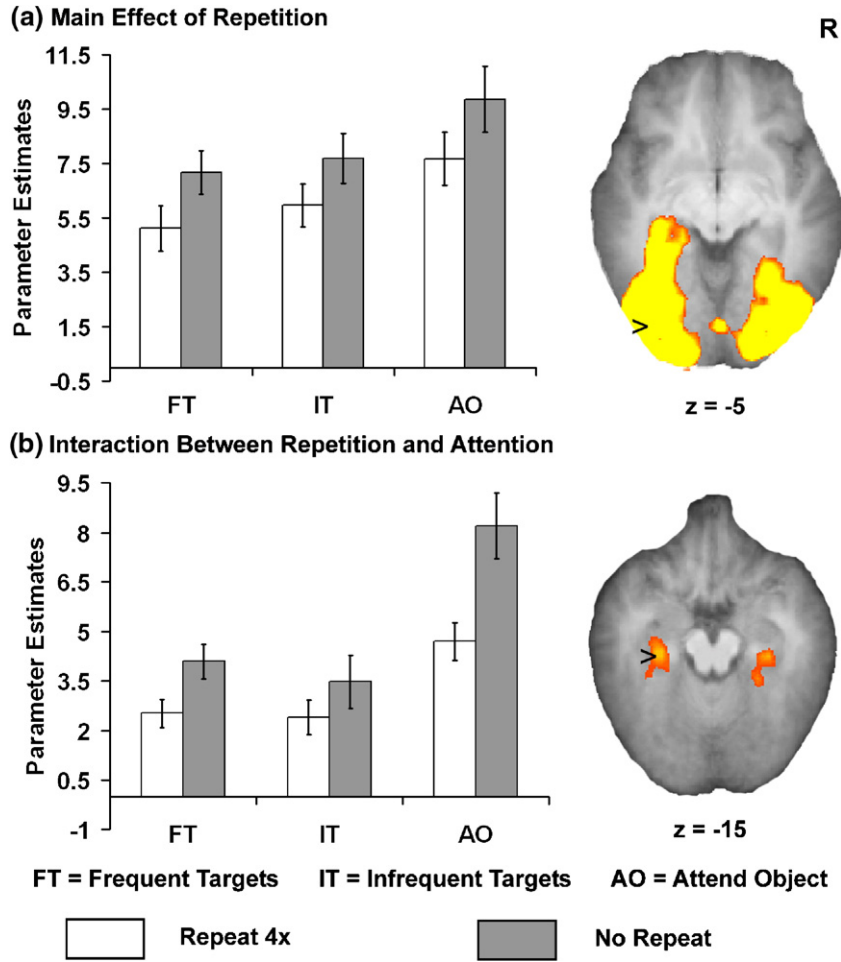


Fig. 4. (a) The upper brain image shows the extensive region along the ventral visual pathway that showed a main effect of adaptation. BOLD signal sampled from the ROI indicated by the arrowhead (see text for basis) showed a significant effect of repetition but not attention. (b) The lower brain map shows the parahippocampal region in which activation showed significant interaction between attention and repetition. BOLD signal sampled here shows that attending to objects yielded significantly higher adaptation than attending to targets. Contrasts were thresholded at  $p < 0.001$  uncorrected.

reflecting higher visual load and higher attentional demands when targets appeared more frequently. However, adaptation magnitude in the ventral visual pathway did not differ between the two target frequencies ( $t(16) < 1$ ).

To determine how the location of adaptation was affected by attention, we performed a two-way ANOVA with attention and repetition as within-subjects factors. We found adaptation to be higher in bilateral parahippocampal and anterior fusiform regions for attended than for unattended objects. (Talairach coordinates:  $-24, -40, -8$ ; Table 1, Fig. 4b).

To clarify the direction of the interaction between attention and locale of adaptation, we compared spherical ROIs obtained from two anterior locations in the parahippocampal gyrus (highlighted above) with two posterior regions (Fig. 4a small arrowhead; left inferior occipital gyrus: Talairach coordinates:  $-36, -80, -5$  and right inferior occipital gyrus; Talairach coordinates:  $36, -70, -5$ ). In contrast to the anterior regions, these posterior regions showed adaptation that was NOT modulated by attention.

The terms ‘anterior’ and ‘posterior’ reflect the regions’ position on axial brain slices. In this work, we chose not to be wedded to the use of functional localizer scans in light of recent controversy regarding their use (Friston et al., 2006). In any case, there was no a priori reason to define a specific area in either the parahippo-

campal region or the lateral occipital cortex, where we expected to see explicit memory effects.

Experiment 2: behavioral results

Repetition facilitated both implicit and explicit memory. Behavioral priming for repeated objects was reflected by shorter response times to repeated objects ( $t(19) = 17.01, p < 0.001$ ; Table 2). Recognition for repeated objects was similarly better ( $t(19) = 6.43, p < 0.001$ ). The volunteers took equally long to judge subsequently remembered and forgotten objects (mean RT for remembered vs.

Table 1  
Talairach coordinates of regions that showed an interaction between target and object repetition (random effects analysis, threshold  $p < 0.001$  (uncorrected))

	BA	Talairach coordinates			F value
		x	y	z	
L parahippocampal gyrus	35	-27	-25	-17	19.86
R parahippocampal gyrus	36	57	11	25	12.82
R lingual gyrus	19	12	-49	1	20.00
L angular gyrus	39	-54	-61	34	15.96

forgotten: 634 ms vs. 639 ms;  $t(19) < 1$ ; note that this refers only to the first object in an object pair as only these were tested). There was no interaction between priming and subsequent recognition memory.

### Experiment 2: imaging results

#### *Ventral visual areas showing a correlation between explicit memory and adaptation*

Across the 20 volunteers, we found a positive correlation between A' and adaptation magnitude in both left and right parahippocampal regions (Talairach coordinates, right 27, -28, -14, left -27, -12, -17;  $r=0.67$ ;  $p<0.001$ ; Fig. 5b), as well as in both lateral occipital regions (Talairach coordinates, right 33, -76, 16, left -42, -82, 16) with A' ( $r=0.51$ ;  $p<0.05$ ).

#### *Ventral visual areas showing a correlation between priming and adaptation*

In contrast to the ventral visual areas showing a correlation between explicit memory and adaptation, the correlation between adaptation and repetition priming ( $r=0.56$ ;  $p<0.05$ ) was present more posteriorly, along a large tract of the fusiform region (peak Talairach coordinates, right 26, -73, -11, left -36, -58, -17) on both sides. The regions showing correlations with priming were more extensive than those showing correlations with explicit memory. There was some overlap in the regions demonstrating the correlations between adaptation and explicit and implicit memory within the anterior fusiform.

Considering the correlations with both explicit and implicit memory, it was striking that only a subset of the many regions of the ventral visual pathway showing short-latency repetition effects (Compare Fig. 4a with Figs. 5a, b) demonstrated adaptation of mnemonic significance.

#### *Activation magnitude and memory measures*

We next evaluated the relationship between activation magnitude and memory. Higher activation strength in a number of regions, including the ventral visual pathway, parietal and frontal lobes, over the memory trial duration has been shown to result in greater likelihood of remembering that trial (Pessoa et al., 2002). We found strong correlations between activation strength across subjects and both explicit ( $r=0.76$ ;  $p<0.001$ ) and implicit ( $r=0.53$ ;  $p<0.05$ ) memory in separable regions along the ventral visual pathway (Fig. 5a). Again, the regions showing stronger correlations with explicit memory lay anterior to those correlating with implicit memory.

In the regions showing good correlation for explicit and implicit memory, individuals exhibiting higher activation also showed higher adaptation ( $r=0.69$ ;  $p<0.001$ ).

A stronger case for distinguishing the contributions of activation and of repetition suppression/adaptation effects on memory could be made by post hoc sorting of encoding events

according to whether they were subsequently remembered and by direct evaluations of the correlation between the two measures of memory (Wagner et al., 2000). However, this is not possible with short-latency repetition designs because of the opposing effects of the stronger encoding-related activation during an initial presentation and the lower signal encountered with repetition of that stimulus. This results in the negation of the subsequent memory effect but not adaptation (Supplementary Fig. 1).

### Discussion

#### *Attention modulates adaptation—in some but not other brain regions*

We found that in the anterior part of the fusiform and parahippocampal regions, adaptation was strongly modulated by attention. In contrast, in the posterior part of the ventral visual pathway, in the lateral occipital and posterior fusiform areas, attention enhanced activation but did not appreciably modulate adaptation. One view is that the latter occurred because we did not completely suppress attention leakage, and some of the attention was directed towards processing of the secondary stimulus, (cf. Eger et al., 2004; Murray and Wojciulik, 2004; Yi and Chun, 2005; Henson and Mouchlianitis, 2007). However, an alternative explanation is that the repetition effects seen in the attend targets condition relate to perceptual processes, but not those involved in building durable explicit memories. These may decay rapidly with the insertion of additional intervening stimuli (Brozinsky et al., 2005; McMahan and Olson, 2007) or be perturbed by emotionally distressing ones (Dolcos and McCarthy, 2006). Could the location rather than the presence of adaptation alone be important in determining memory?

#### *Spatial specificity of where adaptation tracks long-term memory*

Neurophysiological and imaging studies indicate that information flow proceeds along the ventral visual pathway, corresponding to a greater conscious awareness of a stimulus and explicit memory the further along the processing chain the information is transmitted. For example, following repeated brief masked exposures to a stimulus, the activation of the anterior fusiform, parahippocampal gyrus and anterior LOC, but not of the more posterior regions (V1, V2, posterior) corresponds to explicit item recognition (Bar et al., 2001). This is reminiscent of the finding that receptive fields enlarge as one traverses the ventral visual pathway and that more complex and abstract features are coded in higher regions, like IT (Kobatake and Tanaka, 1994). Indeed the type of memory supported at different locales along the pathway may differ, with the early visual cortex and the adjacent regions contributing to unconscious memory, and the 'late visual processing regions', anterior fusiform and parahippocampal contributing to implicit (Ganel et al., 2006) and/or explicit memory (Slotnick and Schacter, 2004, 2006), thus corresponding to the more invariant properties of neural coding here (Schacter et al., 2007).

#### *Short-lag repetition effects as a marker of likelihood of remembering*

It is presently unclear if short-lag repetition effects evaluate the same neural processes as repetition over a longer lag (Bentin and Moscovitch, 1988; Nagy and Rugg, 1989; Henson et al., 2004).

Table 2  
Behavioral performance in Experiment 2

	Mean RT (SD)				Recognition performance A' (SD)
	Remembered (ms)		Forgotten (ms)		
	RT1	RT2	RT1	RT2	
Repeat	721 (146)	488 (150)	760 (257)	509 (199)	0.93 (0.06)
No repeat	678 (128)	647 (202)	679 (120)	611 (205)	0.89 (0.06)

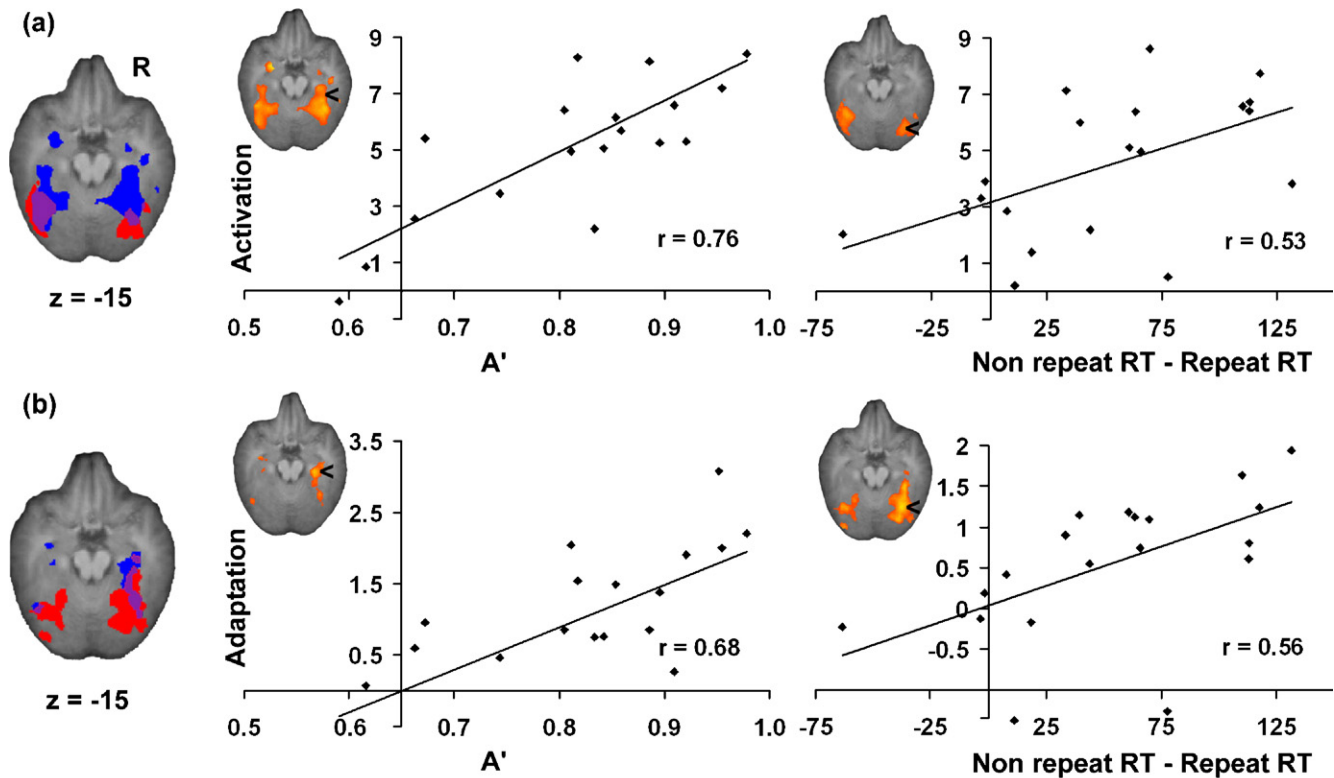


Fig. 5. Correlations between activation, adaptation, subsequent memory ( $A'$ ) and repetition priming. There was a significant correlation between  $A'$  and the magnitude of activation as well as adaptation in the bilateral parahippocampal, anterior fusiform and anterior lateral occipital regions. This correlation was mapped in blue. The correlation between behavioral priming and adaptation magnitude was more extensive and located in the posterior fusiform and posterior lateral occipital region. Areas showing significant correlation with priming are shown in red. All areas shown have positive correlations that were significant at  $p < 0.05$ .

Although there appear to be no major qualitative differences in adaptation as a function of repetition lag in human fMRI data (Henson et al., 2004), primate electrophysiology data suggest otherwise (Baylis and Rolls, 1987; McMahon and Olson, 2007). Repetition effects involving short lags and no intervening stimuli result in larger signal differences between novel and repeated items.

The present study stands out among those addressing the correspondence between adaptation and long-term memory. We used a short repetition lag of under 1 s and evaluated explicit memory. Our observations indicate that people with better explicit memory of visual stimuli engage encoding mechanisms differently from poorer performers. The difference is evident in the peristimulus period. The better performing individuals showed both larger responses to novel stimuli and greater adaptation to repeated stimuli. We suggest that heightened attention during the peristimulus period drives both these phenomena, consistent with the observation that within the PPA, attention to both initial and repeated stimuli modulates the adaptation magnitude (Yi and Chun, 2005; Henson and Mouchlianitis, 2007).

Behavioral work has suggested a close relationship between attention and short-term memory capacity (Awh et al., 2006). Neuroimaging evidence suggests that increased activity at the prestimulus or peristimulus periods in regions involved in perception, encoding and control of attention results in better behavioral performance (Pessoa et al., 2002; Sapir et al., 2005; Sylvester et al., 2006). Additionally, with specific reference to

adaptation experiments, the preliminary data suggest that higher peristimulus 'tonic' neural activity, possibly relating to higher levels of attention at encoding, corresponds to better explicit memory performance at test (Turk-Browne et al., 2006).

#### *Activation, adaptation and differences between implicit and explicit memory*

Clinical neuropsychological data support the existence of separate neural substrates that underpin the retrieval of implicit and explicit memories (Graf and Schacter, 1985). However, common encoding neural substrates for and positive associations between these two types of memory have been demonstrated in the fusiform and parahippocampal regions (Turk-Browne et al., 2006). Here, we observed shared as well as separate areas where adaptation correlates with explicit and with implicit memory within the ventral visual pathway. The present work also differentiates between the locations where explicit and implicit memory best correlate with activation. We found a correspondence between regions involved in specific memory types across both activation and adaptation.

Overall, our findings suggest that although adaptation reflects the extent to which the brain processes a recently viewed stimulus, it is likely to index different processes along the ventral visual pathway depending on the task used. Regions at the top of the ventral visual processing hierarchy appear to manifest activation and adaptation that are most strongly influenced by attention.

These are also the regions showing significant correlations between adaptation magnitude and explicit memory performance. Hence, taking note of where adaptation occurs and the relationship between adaptation and attention are important in assessing the relevance of adaptation to long-term memory.

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### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2007.07.006.

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