Published in final edited form as:

Neuroimage. 2007 February 15; 34(4): 1723–1732.

Spatial Dynamics of Masked Picture Repetition Effects

Marianna D. Eddy^{a,*}, David Schnyer^{b,c}, Annette Schmid^a, and Phillip J. Holcomb^a

*a*Department of Psychology, Tufts University, 490 Boston Avenue, Medford, MA 02155, USA

*b*Memory Disorders Research Center, Boston VA Healthcare System and Boston University School of Medicine, MA 02130, USA

*c*Athinoula A. Martinos Center for Biomedical Imaging, MGH/MIT/HMS, MA 02129, USA

Abstract

The aim of this study was to further elucidate the mechanisms of early and automatic object processing using a masked picture priming paradigm with both identity and exemplar repetition in functional MRI (fMRI). Masked repetition priming has been commonly used with words to isolate automatic, rapidly occurring mechanisms involved in visual word recognition; however, studies using the technique of masked priming with rapid presentation of pictures have been limited. This study demonstrates how the masked priming technique can be used to study early, automatic processing of rapidly presented complex objects. Temporal-occipital regions previously found to be sensitive to repetition priming in both masked word and unmasked picture studies were found to show repetition suppression for the identity primes only. Most notably, when divided into anterior and posterior divisions, the fusiform gyrus showed anatomically specific repetition suppression only in the posterior portion. This finding is comparable to that found in a previous study of masked word priming, and the similarity may suggest an overlap in the early identification processes for visual word form and visual object processing in this region. Finally, masked repetition of different exemplar objects did not result in reliable neural effects, suggesting that the underlying mechanisms of the more semantic-based, different exemplar priming may occur later or require the intervention of conscious processes.

Keywords

fMRI; Masked priming; Repetition priming; Picture processing; Repetition suppression

Introduction

The human visual system can rapidly process and identify objects on the order of a few hundred milliseconds. A complete understanding of the neural and perceptual processes that underlie human object recognition has proven difficult, in part because few techniques have sufficient temporal and spatial resolution to decompose the elemental components involved in recognition. Recently, Dehaene and colleagues (2004) have demonstrated that by combining fMRI recording with the masked repetition priming technique, it is possible to isolate the neuroanatomical substrates involved in the rapid bottom-up processing of visually presented words (Dehaene et al., 2004). In the current study, we extended the Dehaene et al. technique to the domain of object recognition, and report data from an experiment that is the first to combine fMRI recording and masked repetition priming with pictorial stimuli.

*Corresponding author. Fax: +1 617 627 3181. E-mail address: Marianna.eddy@tufts.edu (M.D. Eddy). Available online on ScienceDirect (www.sciencedirect.com).

Various studies have established the neuroanatomical pathway involved in early and middle-level processing of visual stimuli. For this study we focused on the classic ventral system (Ungerleider and Mishkin, 1982) that cascades from V1 through V2 as well as V4 to the posterior TE and then to the entire TE (for a review see Tanaka, 1997). Yaginuma et al. (1993) have found that in monkeys, lesions to the TE, and along the pathway from V1 to TE, lead to disruptions in object recognition. These middle- and high-level processes involved in object recognition have also been studied in humans using fMRI in word and picture priming paradigms (e.g., Bar et al., 2001; Dehaene et al., 2001; Koutstaal et al., 2001).

Masked priming is characterized by a rapid presentation of stimuli. Typically the prime is presented very briefly and is immediately preceded and followed by a pattern mask and then a subsequent target stimulus (which is presented in the clear). This technique has been used in numerous behavioral studies to help decompose the time course of early word processing (Forster and Davis, 1984; Neely, 1991). The logic of this procedure is that the brief presentation of the prime event begins to activate representations in the visual system associated with the prime, but that the onset of the following mask stimulus interrupts processing of the prime prior to the level of conscious identification. By immediately following the mask with a target stimulus that is either the same or different than the prime, it is possible to probe for residual prime influence on the system by looking for subtle differences in target processing. By systematically manipulating the interval between the prime and target (what is called the SOA) and/or the duration of the prime itself, it is possible to infer different characteristics of early perceptual processing. The typical behavioral effect is that target processing is facilitated (e.g., RT for the target is faster) when the prime and target are the same stimulus or share certain features, compared to when they are different, “unrelated” stimuli (e.g., Bar and Biederman, 1998).

More recently, this paradigm has been adapted by Dehaene and colleagues for use with fMRI to examine the brain structures associated with early, automatic word processing. fMRI lacks temporal resolution due to the sluggish nature of the hemodynamic signal (Logothetis et al., 2001; Logothetis and Wandell, 2004), and therefore results are typically ambiguous with respect to whether a particular effect is due to feed-forward neural activity, recurrent feedback activity from higher brain areas, or both. As a possible solution to this, Dehaene et al. (2004) have argued that the mask priming technique, which effectively blocks feedback processing (Lamme and Roelfsema, 2000; Lamme et al., 2002), is a more precise tool for isolating brain structures involved in early recognition processes that are feed-forward (bottom-up) rather than feedback (top-down). In the current study we exploit this feature of masked priming to examine brain areas involved in early bottom-up aspects of object recognition.

Many fMRI studies have examined unmasked priming where both the prime and the target are available to conscious strategies (e.g., Buckner et al., 1998; Koutstaal et al., 2001; Vuilleumier et al., 2002); while relatively few studies have used the masked priming technique, particularly with visually presented objects. With relatively few masked picture priming studies, masked priming studies of words can nonetheless provide us with information about the similarities and differences of the processes involved in masked and unmasked priming.

In a recent language study, Dehaene et al. (2001) compared masked and unmasked repetition priming in words while participants made semantic decisions. Repetition suppression, similar to that seen in unmasked priming studies (decreases in the BOLD signal for repeated stimuli in comparison to unrepeated stimuli), was observed for masked primes as well. There was a greater reduction in activity for visible words when they were preceded by the same masked word as compared to words preceded by a different masked word. Differences in activation were undetectable in prefrontal and parietal areas, presumably reflecting the participants’ inability to report masked words. For repeated stimuli, where a masked prime was matched

with an unmasked target, reductions were seen in the extrastriate cortex, fusiform and precentral gyri. The activation in the right extrastriate cortex was dependent on perceptual manipulations (i.e., lower case versus upper case). In the unmasked condition, the pattern of repetition-related changes was different, with an increase of activity evident in parietal, prefrontal and cingulate sites when compared to masked words. In the ERP portion of their experiment, only a P300 was observed for the unmasked condition and, therefore, they concluded that this may reflect the updating of consciousness (Dehaene et al., 2001).

Dehaene and colleagues (2004) contrasted these earlier results with a follow-up study where they examined masked word priming repetition effects for repeated words in the same retinal location and repeated words in different retinal locations. In the anterior and middle fusiform gyrus, repetition effects were seen for the same word, even when shifted by one letter position. Dehaene et al. (2004) suggested that, while the anterior and middle fusiform seem important in the coding of invariant features, the posterior fusiform effects support a more location-specific letter priming. They attributed the differential effect in the anterior-posterior subdivision of the fusiform to fusiform neurons that become progressively tuned from visual features in extrastriate cortex to larger units, such as graphemes or even words, as one moves anteriorly through fusiform gyrus. Since the right occipitotemporal cortex was only sensitive to repeated stimuli, the authors concluded that it is involved in processing low-level visual features, while a more abstract coding is performed by the left ventral occipitotemporal cortex where cross-case priming occurred.

In contrast to Dehaene's work, Schnyer et al. (2002) observed repetition enhancement in their masked word repetition priming fMRI study. They hypothesized that if reductions in activation seen for unmasked repetition priming reflect facilitated perceptual processing, then these reductions should be observed in masked priming. However, if they are due to "post-identification attentional modulation," then reductions may not be seen in masked priming (where there is no prime identification occurring). Following this line of reasoning, it might be suggested that differences in the pattern of increases and decreases in the fMRI signal associated with repetition may occur due to two processes: one earlier in the processing stream prior to identification and one later after identification has occurred.

While there has not been a report of masked priming with rapidly presented pictures using fMRI, a number of studies have examined the neural effects of picture repetition using supraliminal (unmasked) stimuli and lagged repetition (i.e., primes and targets separated by multiple intervening items). Using real and nonsense objects, Vuilleumier and colleagues (2002) examined repetition effects with objects of the same name, but with some difference in visual form. Decreases associated with repetition were observed in the bilateral inferior temporal gyri and posterior fusiform cortex, extending laterally into the right inferior occipital gyrus for both real and nonsense objects. The second presentation of real objects produced decreased activity in the bilateral fusiform and inferior frontal cortex. Repetition of different exemplars with the same name did not produce effects in the fusiform regions, from which Vuilleumier et al. (2002) concluded that the repetition effects observed for repeated real objects are the result of specific visual representations, not those reflected at a more abstract level such as lexical or semantic representations. Overall, the posterior fusiform was most affected (repetition-related decreases) by the repetition of real objects. The anterior fusiform was more engaged for meaningful stimuli since greater effects were observed for real objects than for nonsense objects. These effects were in the form of repetition suppression for repeated stimuli compared to the first exposure of the stimuli.

Two other studies found differences in the fusiform region when repetition of different exemplars was examined. Koutstaal et al. (2001) examined the neural correlates of visual object priming while participants made size judgments to pictures of objects that were exact

repetitions or were different exemplars of items previously seen. They found repetition-related reductions across a wide range of brain regions in frontal and posterior areas. Of particular interest here was the modulation of the magnitude of repetition-related changes that occurred in the bilateral middle occipital, parahippocampal, and fusiform cortices when repetition spanned different visual exemplars. Occipitotemporal cortex (fusiform) showed laterality differences in sensitivity to identity/exemplar status, so that there was less repetition reduction for different exemplars in the right fusiform.

Similarly, Simons et al. (2003) found less repetition reduction in the right fusiform than in the left fusiform for repeated different exemplars. They argued that the left fusiform gyrus is more sensitive to lexical/semantic aspects of the stimuli while the right fusiform gyrus is more sensitive to perceptual form. Simons et al. (2003) also reported greater repetition reduction for different exemplars in the left occipitotemporal cortex. They interpreted this finding to indicate an increasing sensitivity to the complexity of object representations when moving from posterior to anterior locations in the left occipitotemporal cortex.

One possible reason for the discrepancy between Vuilleumier and colleagues findings with different exemplars and other studies involving different exemplar priming (Koutstaal et al., 2001; Simons et al., 2003) could be the difference in number of repetitions. While Simons et al. (2003) and Koutstaal et al. (2001) both have multiple repetitions of the stimuli, the Vuilleumier study used a single repetition.

The previously mentioned studies of supraliminal picture priming combined with the studies of masked word priming, suggest that there might be an overlap in the early visual areas utilized during word and picture recognition. However, several questions remain. First, the previous picture studies all used lagged repetition, which is known to modulate both perceptual and memory-based processes (Forster and Davis, 1984), thus leaving it unclear which of the observed effects are specific to object perception. Second, the use of supraliminal presentation in fMRI studies renders conclusions about the time course of repetition priming effects somewhat unclear (i.e., whether they are due to initial bottom-up processing, subsequent top-down processing or a combination of the two—see Dehaene et al., 2004). Interestingly, a recent event-related potential (ERP) study found evidence for early masked repetition effects to pictures of repeated objects (N/P190—Eddy et al., 2006), suggesting that masked repetition priming effects can be observed for single repetitions at short prime-target intervals. However, because of the relatively poor spatial resolution of ERPs, the authors were not able to locate the precise anatomical locus of their effects.

The current experiment aimed to examine the neuroanatomical loci of object repetition effects in an event-related fMRI design. Specifically, from this study we hoped to better understand which areas in the visual processing stream are affected by rapidly presented masked picture presentation and, more specifically, identify the underlying neural loci and mechanisms involved in identity repetition priming, as well as repetition of different exemplars. In summary, this experiment aims to address the following questions:

1. Do masked repetitions of pictures produce suppression or enhancement in the BOLD signal?
2. Is there evidence of an anterior-posterior dissociation within the fusiform gyrus in the response to masked picture repetitions?
3. Is the functional neuroanatomy involved in masked picture priming a subset of the neuroanatomical loci involved in unmasked picture priming or are they separate substrates?

4. Is there any evidence for masked repetition effects between different object exemplars or are such presumably semantically mediated effects dependent on identification of the prime (since the different exemplars share fewer physical similarities than the repeated exemplars, but have more semantic relatedness than the unrepeated condition)?

Materials and methods

MRI participants

Seventeen Boston area undergraduates (8 females; mean age = 20.47 years) participated in this study for monetary compensation. They were all right handed with no history of neurological or psychiatric disorder, with normal or corrected-to-normal vision. Written informed consent was obtained from all participants. All procedures were approved by the Massachusetts General Hospital Human Studies Committee.

Stimuli

Real pictures of everyday objects were used in this experiment from Hemera photo-objects (<http://www.hemera.com>). All pictures were conventional views of the objects on a white background. There was a total set of 480 critical pictures (240 exemplar pictures and 240 different exemplars) and 120 non-critical pictures (60 filler items and 60 food items). The different exemplar pairs were selected to elicit the same name, but have different physical attributes (shape, color etc.; see Fig. 1 for examples). All different exemplar pairs were checked by several raters for name agreement. Pictures were divided up into groups of 60 and rotated through each of the conditions of interest for the eight lists. A control condition consisting of an average luminancy of the pictures occurred in the prime and target positions (60 per list). The control stimulus is a visually similar picture that lacks semantic properties (see Fig. 1). Also, a null condition of fixation (20% of total trials) was presented for varying amounts of time in order to create jitter in the stimulus presentation. The order of conditions was optimized and an event-related design was used.

In total each subject viewed 300 pairs of pictures. There were 60 picture pairs in condition 1 (repeated), 60 picture pairs in condition 2 (different exemplar), 60 picture pairs in condition 3 (unrelated), and 60 “probe” picture pairs (which served as the category for making the button pressing response) and 60 picture pairs of the control condition. Thirty of the probe pictures were placed in the masked prime position (to check for the effectiveness of masking) and 30 were placed in the visible target position. There were eight completely counterbalanced lists; therefore, differences in color, orientation, or other physical attributes of pictures are cancelled out through this counterbalancing (since every picture appears in every condition throughout the eight lists). The order of each exemplar in the different exemplar condition was also counterbalanced. All stimuli were randomized and presented in an optimized sequence using the optseq program of the FreeSurfer Functional Analysis Stream (FS-FAST) analysis tools.

Stimuli were presented with a forward and backward mask, with a prime presented for 53 ms in between. The forward mask was presented for 293 ms and the backward mask was presented for 53 ms (13 ms inter-stimulus interval (ISI)). The target was then presented for 293 ms. The stimulus onset asynchrony (SOA) between the prime and target was 119 ms. Participants were asked to respond by pressing a button resting in their lap when they detected a food item in either the prime or target position. Participants were given clear instructions on what constituted a food item (e.g., live animals are not food items; food-related items are not food items). A refresh rate of 75 Hz was used with a screen resolution of 1024 × 768.

MRI acquisition

fMRI parameters—Participants were scanned at the Athinoula A. Martinos Center for Biomedical Imaging, Massachusetts General Hospital on a 3-TSiemens Trio system using a Siemens 8-channel head coil. Functional data were collected using a gradient-echo echo-planar pulse sequence (TR = 2000 ms, TE = 30 ms, 23 axial slices, $2 \times 2 \times 2.5$ mm, 0.2 mm interslice gap, 96×96 acquisition matrix). The slice prescription was chosen to maximize the signal in the temporal lobes. The resolution of the voxels during the functional runs did not allow for whole brain coverage. Anatomical scans (3D T1-weighted MPRAGE volumes) were acquired prior to functional scanning for anatomical co-registration with fMRI data (TR = 7.3, TE = 3.2 or 3.0, flip angle = 7° , slice thickness = 1.3 mm, 128 slices, FOV = 256×256 mm).

Procedure—Participants viewed pictures projected onto a screen at the end of the bore through a mirror mounted on the head coil. Prior to beginning the functional runs, approximately 10 min of structural scans were done. Participants were given an opportunity to practice the task while in the scanner with other non-overlapping stimuli. The functional scans consisted of 6 runs of 4 min each, allowing participants to rest in between. Awareness was assessed through the number of responses to food (probe) items in the prime position.

Data analyses—The fMRI data were analyzed using Freesurfer (FS-FAST stream). Data were motion corrected, smoothed with a 6-mm Gaussian filter, and intensity normalized before estimation of the event-related responses was accomplished using a fixed impulse response model. High-resolution MPRAGE images were segmented and cortical regions were defined using an automated surface-based analysis that transformed each individual's brain into a common spherical coordinate system (see Dale et al., 1999; Fischl et al., 1999 for the details of procedure). Each individual's fMRI results were aligned with their structural images and transformed into spherical coordinates. Automated parcellation of each individual's spherical surface provided anatomical labels for the region of interest (ROI) analysis (see Fischl et al., 2004 for the details of parcellation).

Results

Masked picture repetition effects were investigated using an event-related fMRI experiment. There were three critical conditions of interest: repetition where the masked prime and target were the same object, repetition with a different exemplar where the masked prime had the same name as the target, but had a different physical form, and unrepeated where the masked prime and target shared no physical or semantic similarities. Seventeen participants made button presses to non-critical food items (see Fig. 1 for schemata of typical trials). Participants responded 97% of the time to the food targets, but only detected 15% of the food primes. While this target detection task has the disadvantage of having no behavioral index of priming, it avoids the possible confound of priming effects being due to response learning (see Dobbins et al., 2004). Two types of analyses were performed on the data: a group random effects analysis on the cortical surface and a more anatomically specified region of interest (ROI) analysis constrained by voxels active during picture identification.

Cortical surface-based analysis

Direct pairwise comparisons between priming conditions were computed from random effects group averages where significant differences between conditions were determined across timepoints 4–6 s post stimulus onset (PSO; Fig. 2). The areas that showed a greater response to all pictures compared to the control condition and had voxels whose hemodynamic response fit a pre-designated gamma function can be seen in Fig. 2A. Temporal and occipital areas showed greater activation for pictures of objects in comparison to the control picture from 4–6 s PSO. Directly comparing individual conditions, these random effects displayed on an inflated

cortical surface are observed in a smaller subset of temporal and occipital areas for unrepeated pictures (unprimed) compared to repeated pictures (primed). In the third comparison, relatively few areas except for a small ventral temporal area show greater effects for unrepeated pictures (unprimed) compared to different exemplars when doing cortical surface-based analyses.

Regions of interest (ROI) analysis

ROIs were defined on each individual subject's inflated surface using an automated parcellation (see Fischl et al., 2004 for details). This automated parcellation method uses probabilistic information estimation from a manually labeled training set. Fischl et al. (2004) found this method to be similar in accuracy to manually labeling the cortical surface. A random effects group average was computed for voxels whose hemodynamic response fit a pre-designated gamma function and showed greater activation in the 3 object conditions (repeated, unrepeated, different exemplar) versus the control picture and was used as a functional constraint for the anatomically defined ROIs (see Fig. 3) thresholded at $p < 0.001$. Since a previous study of masked priming for words (Dehaene et al., 2004) and a study of pictures (Simons et al., 2003) resulted in anterior-posterior differences in the fusiform gyrus, the fusiform gyrus was divided into anterior-posterior portions by dividing each individual subject's fusiform in half on the inflated spherical surface; this was done by measuring the length of the fusiform and dividing it exactly in half (see Fig. 3 for ROIs; Fig. 4 for time course of fusiform). The remaining ROIs were not divided.

Various regions showed greater activation for the pictures as compared to the control condition including: the fusiform gyrus, posterior inferior temporal gyrus (ITG), inferior occipital gyrus, middle occipital gyrus, temporal occipital medial lingual gyrus, occipital pole, posterior transverse collateral sulcus, and middle occipital sulcus and Lunatus (see Fig. 2A). Effects of masked repetition priming were examined in these regions by extracting the mean percent signal change, across timepoints 4-6 s PSO, which was then baselined to an average of the 4 s pre-stimulus period and submitted to repeated measures ANOVA. Each region was examined separately with hemisphere and condition as within subjects factors, with an additional factor of location (anterior-posterior) added to the fusiform analysis. Of these regions, the fusiform gyrus, middle occipital gyrus and posterior ITG revealed significant effects of repetition when making a comparison across the three conditions.

The main comparisons done for this study were between the repeated pictures and unrepeated pictures (repetition priming), and between the repeated different exemplar pictures and unrepeated pictures (different exemplar repetition priming). Overall 2×2 ANOVAs between these conditions were performed that included condition and hemisphere as variables for each of the regions listed above, with the exception of the fusiform, where a $2 \times 2 \times 2$ ANOVA was performed including the additional variable of position in the fusiform (anterior or posterior).

Same exemplar repetition priming effects

When comparing repeated to unrepeated pictures in the fusiform gyrus, a $2 \times 2 \times 2$ ANOVA revealed a main effect of condition ($F(1,16) = 7.855, p = 0.013$) and a main effect of position ($F(1,16) = 22.617, p = 0.000$). Additionally, an interaction between condition and position ($F(1,16) = 7.622, p = 0.014$) was observed for the repetition priming condition. Upon examination of the means for each condition relative to position, these effects were driven by a decrease in percent signal change in the posterior fusiform for repeated pictures compared to unrepeated pictures. However, these effects were not observed in the anterior fusiform as demonstrated by pairwise comparisons between conditions in the anterior fusiform ($p > 0.05$) compared to the posterior fusiform ($t(16) = -3.133, p = 0.006$).

When comparing the percent signal change for these two conditions in a 2×2 ANOVA in other ROIs, several areas showed main effects of condition. The regions that showed significant differences between the repeated and unrepeated conditions as demonstrated by a main effect of condition were the inferior occipital gyrus ($F(1,16) = 4.878, p=0.042$), middle occipital gyrus ($F(1,15) = 7.879, p = 0.013$), the temporal occipital medial lingual gyrus ($F(1,16) = 5.495, p = 0.032$) and the middle occipital sulcus and Lunatus ($F(1,16) = 6.759, p = 0.019$). The occipital pole and posterior collateral transverse sulcus did not show any significant differences between these conditions or any interactions ($p > 0.08$).

Different exemplar repetition priming effects

Within the fusiform gyrus, there were no significant effects when comparing percent signal change for repeated different exemplars to unrepeated pictures in a $2 \times 2 \times 2$ ANOVA ($p > 0.1$). Furthermore, no other regions showed effects ($F < 2$ or $p > 0.1$) for comparisons between these conditions except for the posterior ITG. A 2×2 ANOVA on the data extracted from the posterior ITG revealed an interaction between condition and hemisphere ($F(1,14) = 28.432, p = 0.000$), where the different exemplar condition showed greater percent signal change than the unrepeated condition in the left hemisphere and less percent signal change than the unrepeated condition in the right hemisphere. Main effects of condition and hemisphere were not significant. This interaction effect was driven by a difference of the repeated different exemplar condition between the right and left hemisphere ($t(14) = 2.616, p = 0.020$). Pairwise comparisons did not show any differences between the repeated different exemplar and unrepeated conditions within the right or left hemispheres.

Summary of results

Overall, the fusiform gyrus revealed repetition-related suppression of the BOLD signal when comparing items preceded by a masked identity prime (repeated condition) and those preceded by a masked unrepeated object. Several other occipitotemporal regions revealed a similar suppression of neural activity for the repeated condition compared to the unrepeated condition with the exception of earlier visual areas such as the occipital pole and posterior transverse collateral sulcus. Only one area, the posterior ITG, showed a reliable effect in the different exemplar condition, the condition where the target object was preceded by a masked prime of a different exemplar of that object. The interaction of condition and hemisphere in this region reflects a differential response to objects preceded by a masked different exemplar between the left and right hemispheres where different exemplars have an intermediary level of activation in the right hemisphere in comparison to unrelated and repeated picture pairs.

Discussion

This experiment examined the effects of briefly presented masked pictures on the early and presumably bottom-up (automatic) processing of visual objects. Overall, the results revealed clear effects of masked picture priming within the ventral-temporal processing stream, up to and including the posterior fusiform gyrus. When comparing masked repeated pictures to masked unrepeated pictures, repetition suppression was observed in the inferior occipital gyrus, middle occipital gyrus, middle occipital sulcus and Lunatus, and temporal occipital medial lingual gyrus. In addition, and as predicted, repetition suppression (not enhancement) was observed bilaterally in the fusiform gyrus. Effects of masked repetition have previously been reported in masked word studies (e.g., Dehaene et al., 2001,2004) and visible repetition picture priming studies (e.g., Buckner et al., 1998;Koutstaal et al., 2001;Zago et al., 2005), but to our knowledge this is the first demonstration of such an effect for masked picture priming with a short SOA between repeated primes and targets. The fact that repetition effects observed in our study are similar to those found in the fusiform gyrus in other priming studies, would

suggest that the masked priming effects stem from processing of visual features associated with the pictures.

When contrasted with the regions where repetition suppression was observed, masked repetition effects were not observed in very early visual areas such as the occipital pole (see Fig. 3 for specific ROI location). This suggests that these early visual regions might not be sensitive to repetition at the presentation rates used in our experiment. Interestingly however, regions involved in higher level visual processing, such as the posterior fusiform, were clearly modulated by item repetition. Such an effect might be expected if there is a more sustained activity (such as reverberation) in these higher level areas (i.e., Grossberg, 1976). Extensive representation of objects is available for several hundred milliseconds after the offset of an image (e.g., Landman et al., 2004), possibly leading to a neuronal adaptation (see Grill-Spector and Malach, 2001). This would suggest that the changes in the hemodynamic response we observed are produced not just by simple, early visual features, since the effects seen here occur relatively late in the visual processing stream. Thus, in our study, repetition suppression effects are observed as information moves along the visual processing path, which would be consistent with Dehaene et al.'s (2004) suggestion that processing of stimuli (in their case words) becomes more tuned to larger and invariant features while moving from posterior to anterior processing cortices.

Importantly, our analysis dividing the fusiform gyrus into anterior and posterior portions showed that the effect of masked picture priming in this region is only observed in the bilateral posterior fusiform, but not in the anterior fusiform. Because Dehaene found that the posterior fusiform was sensitive to masked repetition priming only for items with strong visual overlap, the current findings suggest that early effects of masked picture repetition in the visual stream are due, at least to some extent, to visual similarity. One interpretation of the convergence of masked picture and word effects in the posterior fusiform is that visual word and visual picture processing may overlap in this region of the fusiform during early visual processing.

Additionally, there also seem to be important differences in processing within the fusiform region between the visual processing of words and pictures, as the Dehaene study clearly demonstrated effects of masked word priming in the anterior fusiform; whereas our study did not show an analogous masked picture priming effect. A future study that allows a direct comparison between the effects of masked word priming and masked picture priming could more clearly elucidate the divergence and convergence of word and picture processing in the ventral-temporal processing stream.

The lack of anterior fusiform effects for masked picture priming may suggest a divergence in the selectivity of the stream with respect to how words and pictures are processed possibly supporting the hypothesis that visual words are a specialized form of visual object. While separable neural structures for the processing of words and pictures remain a possibility, other researchers have argued against this type of specificity in processing. Instead it has been argued that what has been labeled as the visual word form area (VWFA), a midfusiform area engaged in processing of words (e.g., Cohen et al., 2002), is responsible for the processing of general stimuli rather than stimuli of a specific type (see Price and Devlin, 2003; Price and Devlin, 2004 for a discussion of this issue). Consistent with this view are studies that have found activation in the VWFA while listening and thinking about the meaning of words, repetition of auditory words (Price et al., 2003), or hearing the definitions of objects (Thompson-Schill et al., 1999). Since these tasks do not involve any word form processing, this has been taken to support the idea of the VWFA as an area that processes general stimuli rather than specifically word form.

Various studies of object identification have suggested that the response to stimuli becomes more selective to stimulus type when moving more anterior towards the middle and anterior inferior temporal cortex (Allison et al., 1994; Puce et al., 1995, 1996). Kanwisher et al. (1997) found that non-face objects activated differential areas compared to faces, specifically the bilateral fusiform gyrus and parahippocampal gyrus. Areas activated more significantly by faces were found to be more anterior in the fusiform and predominately in the right hemisphere, further demonstrating stimulus selectivity when proceeding along the ventral processing stream. Simons et al. (2003) made a similar argument suggesting that processes engaged by the posterior occipitotemporal cortex may be more sensitive to the perceptual aspects of stimuli, while moving more anterior in this region, processing acts on higher levels of visual abstraction and this would be consistent with our findings in the posterior temporal region (see also, Ungerleider, 1995).

The current study also contrasted priming effects when the prime and the target shared semantic attributes (same name), but differed in physical form, with those of unrelated primes and targets. Consistent with findings by Vuilleumier and colleagues (2002) in an unmasked priming paradigm, these different physical form exemplars did not produce reliable masked repetition effects even though their lexical attributes overlapped. Vuilleumier et al. interpreted this lack of a priming effect across different exemplars in the posterior fusiform as evidence that this region is especially important for processing the physical form of the stimuli, but not lexico-semantic properties. This interpretation is also consistent with the results obtained in our masked repetition experiment. Although the main effects of priming across visual exemplars were not found to be reliable, we did find an interaction of hemisphere by the condition in the posterior ITG between repeated and different exemplars. While repeated pictures and different exemplars have overlap between semantic attributes of their primes and targets, the difference observed may be explained by differences in processing of physical form. In the right posterior ITG, different exemplars showed an intermediary level of activation between the repeated (least activation) and the unrepeated (most), which is consistent with the idea that the right occipitotemporal cortex is primarily responsible for the processing of low-level perceptual features of stimuli.

In contrast to the findings here and in Vuilleumier et al. (2002), two other studies have demonstrated repetition suppression for different exemplar priming (Koutstaal et al., 2001; Simons et al., 2003). Simons et al. (2003) have suggested that one possible reason for the discrepancy may be that items in the Vuilleumier study might have low name agreement. However, the results of our current masked priming study cannot be attributed to this since all pairs of different exemplars were checked pre-experimentally for consistency in name agreement. Alternatively, the differences between these four studies could be due to the number of repetitions. Our study, as well as Vuilleumier et al.'s (2002), utilized only a single presentation of the prime before the target presentation, while Koutstaal et al. (2001) and Simons et al. (2003) exposed subjects to multiple repetitions of the prime before exposing them to the tested different exemplar target. Differences in the number of prime presentations may explain these conflicting results as it is possible that multiple, unmasked repetitions may allow for more consistent abstraction away from the visual form and contribute to lexical level priming. These results suggest that areas showing repetition effects are more sensitive to physical attributes of the stimuli than lexico-semantic attributes when the prime is masked. If the ventral processing stream is more sensitive to lexical/semantic attributes as processing moves more anterior, it is possible that the masking did not allow processing of different exemplars to reach this stage, especially after only one repetition. To better interpret these different exemplar results a future study might examine a condition that holds physical form constant, but manipulates lexical/semantic properties (e.g., share physical qualities such as shape, color, but differ in name and have no semantic relationship).

Conclusions

The results of this study suggest that when pictures are presented rapidly and without conscious awareness, repetition suppression, rather than enhancement occurs, possibly reflecting facilitated perceptual processing (see Grill-Spector et al., 2006; Grill-Spector and Malach, 2001). In terms of visual object processing, the results also reveal some important findings with regards to similarities and differences in the way visual stimuli or stimuli that induce mental imagery (such as visual words; auditory words) are processed. The results suggest that while early in the visual processing stream visual words and visual objects might be processed similarly, later in the stream, such as at the level of the anterior fusiform, there is divergence in the processing of these two stimulus types. Finally, the current study failed to reveal priming effects in the fusiform across different visual exemplars, providing evidence that semantic processing is not invoked by a masked picture prime. This study demonstrates how even a brief presentation of visual stimuli can reveal important clues about the rapid and automatic processing that takes place during visual object processing.

Acknowledgments

This research was funded through grants HD025889 and HD043251 to Phillip J. Holcomb and K23MH64004 to David Schnyer. We thank Lindsay Nicholls for her assistance with the data collection.

References

- Allison T, Ginter H, McCarthy G, Nobre AC, Puce A, Luby M, et al. Face recognition in human extrastriate cortex. *J. Neurophysiol* 1994;71(2):821–825. [PubMed: 8176446]
- Bar M, Biederman I. Subliminal visual priming. *Psychol. Sci* 1998;9:464–469.
- Bar M, Tootell R, Schacter D, Greve D, Fischl B, Mendola J, Rosen B, Dale AM. Cortical mechanisms of explicit visual object recognition. *Neuron* 1998;29:529–535. [PubMed: 11239441]
- Buckner RL, Goodman J, Burock M, Rotte M, Koutstaal W, Schacter D, Rosen B, Dale AM. Functional-anatomic correlates of object priming in humans revealed by rapid presentation event-related fMRI. *Neuron* 1998;20:285–296. [PubMed: 9491989]
- Cohen L, Lehericy S, Chochon F, Lemer C, Rivaud S, Dehaene S. Language-specific tuning of visual cortex? Functional properties of the visual word form area. *Brain* 2002;125(Pt 5):1054–1069. [PubMed: 11960895]
- Dale AM, Fischl B, Sereno MI. Cortical surface-based analysis: I. Segmentation and surface reconstruction. *NeuroImage* 1999;9:179–194. [PubMed: 9931268]
- Dehaene S, Naccache L, Cohen L, Le Bihan D, Mangin J-F, Poline J-B, Riviere D. Cerebral mechanisms of word masking and unconscious repetition priming. *Nat. Neurosci* 2001;4:752–758. [PubMed: 11426233]
- Dehaene S, Jobert A, Naccache L, Ciuciu P, Poline J, Bihan D, Cohen L. Letter binding and invariant recognition of masked words: behavioral and neuroimaging evidence. *Psychol. Sci* 2004;15:307–313. [PubMed: 15102139]
- Dobbins IG, Schnyer DM, Verfaellie M, Schacter DL. Cortical activity reductions during repetition priming can result from rapid response learning. *Nature* 2004;428(6980):316–319. [PubMed: 14990968]
- Eddy M, Schmid A, Holcomb PJ. A new approach to tracking the time-course of object perception: masked repetition priming and event-related brain potentials. *Psychophysiology* 2006;43(6):659–667.
- Fischl B, Sereno MI, Dale AM. Cortical surface-based analysis: II. Inflation, flattening, and a surface-based coordinate system. *Neuro-Image* 1999;9:195–207. [PubMed: 9931269]
- Fischl B, van der Kouwe A, Destrieux C, Halgren E, Segonne F, Salat DH, Busa E, Seidman LJ, Goldstein J, Kennedy D, Caviness V, Makris N, Rosen B, Dale AM. Automatically parcellating the human Cereb. Cortex. *Cereb. Cortex* 2004;14:11–22.
- Forster KI, Davis C. Repetition priming and frequency attenuation in lexical access. *J. Exper. Psychol., Learn., Mem., Cogn* 1984;10:680–698.

- Grill-Spector K, Malach R. fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychol* 2001;1071-3:293–321.
- Grill-Spector K, Henson R, Martin A. Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn. Sci* 2006;101:14–23. [PubMed: 16321563]
- Grossberg S. Adaptive pattern classification and universal recoding: I. Parallel development and coding of neural feature detectors. *Biol. Cybern* 1976;233:121–134. [PubMed: 974165]
- Kanwisher N, McDermott J, Chun MM. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci* 1997;17(11):4302–4311. [PubMed: 9151747]
- Koutstaal W, Wagner AD, Rotte M, Maril A, Buckner RL, Schacter DL. Perceptual specificity in visual object priming: functional magnetic resonance imaging evidence for a laterality difference in fusiform cortex. *Neuropsychologia* 2001;39:184–199. [PubMed: 11163375]
- Lamme VAF, Roelfsema PR. The distinct modes of vision offered by feedforward and recurrent processing. *Trends Neurosci* 2000;2311:571–579. [PubMed: 11074267]
- Lamme VA, Zipser K, Spekreijse H. Masking interrupts figure-ground signals in V1. *J. Cogn. Neurosci* 2002;147:1044–1053. [PubMed: 12419127]
- Landman R, Spekreijse H, Lamme VA. Relationship between change detection and post-change activity in visual area V1. *NeuroReport: Rapid Commun. Neurosci. Res* 2004;1514:2211–2214.
- Logothetis NK, Wandell BA. Interpreting the BOLD signal. *Annu. Rev. Physiol* 2004;66:735–769. [PubMed: 14977420]
- Logothetis NK, Pauls J, Augath M, Trinath T, Oeltermann A. Neurophysiological investigation of the basis of the fMRI signal. *Nature* 2001;412:150–157. [PubMed: 11449264]
- Neely, JH. Semantic priming effects in visual word recognition: a selective review of current findings and theories. In: Besner, D.; Humphreys, GW., editors. *Basic Processes in Reading: Visual Word Recognition*. Lawrence Erlbaum Associates, Inc.; Hillsdale, NJ: 1991. p. 264-336.
- Price CJ, Devlin JT. The myth of the visual word form area. *NeuroImage* 2003;19(3):473–481. [PubMed: 12880781]
- Price CJ, Devlin JT. The pro and cons of labelling a left occipitotemporal region: “the visual word form area”. *NeuroImage* 2004;22(1):477–479. [PubMed: 15110041]
- Price CJ, Winterburn D, Giraud AL, Moore CJ, Noppeney U. Cortical localisation of the visual and auditory word form areas: a reconsideration of the evidence. *Brain Lang* 2003;86(2):272–286. [PubMed: 12921768]
- Puce A, Allison T, Gore JC, McCarthy G. Face-sensitive regions in human extrastriate cortex studied by functional MRI. *J. Neurophysiol* 1995;74(3):1192–1199. [PubMed: 7500143]
- Puce A, Allison T, Asgari M, Gore JC, McCarthy G. Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. *J. Neurosci* 1996;16(16):5205–5215. [PubMed: 8756449]
- Schnyer DM, Ryan L, Trouard T, Forster K. Masked word repetition results in increased fMRI signal: a framework for understanding signal changes in priming. *NeuroReport* 2002;13:281–284. [PubMed: 11930123]
- Simons JS, Koutstaal W, Prince S, Wagner AD, Schacter DL. Neural mechanisms of visual object priming: evidence for perceptual and semantic distinctions in fusiform cortex. *NeuroImage* 2003;19:613–626. [PubMed: 12880792]
- Tanaka K. Mechanisms of visual object recognition: monkey and human studies. *Curr. Opin. Neurobiol* 1997;7:523–529. [PubMed: 9287204]
- Thompson-Schill SL, Aguirre GK, D’Esposito M, Farah MJ. A neural basis for category and modality specificity of semantic knowledge. *Neuropsychologia* 1999;37(6):671–676. [PubMed: 10390028]
- Ungerleider LG. Functional brain imaging studies of cortical mechanisms for memory. *Science* 1995;270:769–775. [PubMed: 7481764]
- Ungerleider, LG.; Mishkin, M. Two cortical visual systems. In: Ingle, DJ.; Goodale, MA.; Mansfield, RJW., editors. *Analysis of Visual Behavior*. MIT Press; Cambridge, MA: 1982. p. 549-586.
- Vuilleumier P, Henson R, Driver J, Dolan R. Multiple levels of visual object constancy revealed by event-related fMRI of repetition priming. *Nat. Neurosci* 2002;5:491–499. [PubMed: 11967545]

- Yaginuma, S.; Osawa, Y.; Yamaguchi, K.; Iwai, E. Differential functions of central and peripheral visual field representations in monkey prestriate cortex. In: Ono, T.; Squire, LR.; Raichle, ME.; Perrett, DI.; Fukuda, M., editors. *Brain Mechanisms of Perception and Memory*. Oxford Univ. Press; Oxford: 1993. p. 3-15.
- Zago L, Fenske MJ, Aminoff E, Bar M. The rise and fall of priming: how visual exposure shapes cortical representations of objects. *Cereb. Cortex* 2005;15:1655–1665. [PubMed: 15716471]

Fig 1.
Typical trials for each of the four conditions.

Fig 2.

Random effects group averages in spherical space. (A) Random effects group average was computed for voxels whose hemodynamic response fits a pre-designated gamma function and showed greater activation in the 3 object conditions (repeated, unrepeatd, different exemplar) versus the control picture. (B) Random effects group average over timepoints 4-6 for unprimed (unrepeatd pictures) greater than primed (repeatd pictures); areas in yellow/orange represent repetition suppression. (C) Random effects group average over timepoints 4-6 for unprimed (unrepeatd pictures) greater than different exemplar repetition; areas in yellow/orange represent repetition suppression.

Fig 3.
ROIs defined on one representative subject.

Fig 4. Hemodynamic response in the anterior and posterior fusiform gyrus: percent signal change for the anterior and posterior fusiform gyrus. ROIs defined on a representative subject's inflated spherical surface are shown. Average percent signal change was computed for each condition.