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Repetition effects for words and nonwords as indexed by event-related fMRI:

A preliminary study.

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Running head: Word-nonword repetition effects

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We have previously shown differential effects of stimulus familiarity on the repetition-related responses in right fusiform cortex to both faces and symbols. Repetition of familiar stimuli produced a response decrease, whereas repetition of unfamiliar stimuli produced a response increase. In the present experiment, we used words and nonwords as the familiar and unfamiliar stimuli respectively. In this case, the only fusiform region showing the familiarity-by-repetition interaction was in anterior left fusiform. This finding is consistent with our hypothesis that these repetition-related effects occur in the same regions responsible for recognition of familiar stimuli.

Keywords

EVENT-RELATED FMRI WORD NONWORD REPETITION PRIMING

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Repetition priming - the facilitation or biasing of behaviour caused by repetition of a stimulus, in the absence of any direct reference to that repetition - has been studied extensively by cognitive psychologists. The effects of stimulus repetition on the brain have also been examined with neurophysiological, and, more recently, neuroimaging techniques. The most common finding is a decrease in the mean neural firing rate (e.g., Desimone 1996) or regional haemodynamic response (e.g., Schacter and Buckner 1998), a phenomenon often termed “repetition suppression”. This phenomenon may represent the neural correlate of behavioural priming effects.

In a previous neuroimaging study, we asked whether these repetition effects are sensitive to stimulus familiarity, as defined by whether or not stimuli are likely to have pre-existing representations in memory. This question is important with regard to two prominent psychological accounts of repetition priming: “abstractionist” and “episodic” theories (Bowers, 2000; Tenpenny, 1995). Abstractionist theories assume that priming reflects some residual activation, or reduced threshold, associated with pre-existing representations of stimuli. Examples of such representations include logogens (the lexical representations of words; Morton, 1969), pictogens (abstract representations of familiar visual objects; Warren & Morton, 1982) and Face Recognition Units (structural representations of familiar faces; Bruce & Young, 1986). Episodic theories however assume that the processing of any stimulus is, in principle, sufficient to leave some trace (e.g., create new representations) that can cause subsequent priming. Examples of such theories include the “processing episodes” of Jacoby (1983), the transfer appropriate processing theory of Roediger and Blaxton (1987) and the perceptual representation system of Schacter (1990).

One important distinction between these two classes of theory is whether unfamiliar (novel) stimuli can be primed. According to abstractionist theories, they cannot, because no representation exists to activate and/or modify. According to episodic theories, both familiar and unfamiliar stimuli can be primed (providing the stimuli are processed to a sufficient level). The behavioural evidence relevant to these predictions has been mixed (see, for example, Ellis, Young, & Flude, 1990; Stark & McClelland, 2000; or, for reviews, Bowers, 2000; Tenpenny, 1995).

Our previous study examined repetition effects for faces and symbols in an indirect monitoring task (Henson, Shallice, & Dolan, 2000). Each stimulus was either familiar (e.g., a famous face, or a meaningful symbol) or unfamiliar (e.g., a previously unseen face, or a meaningless line-drawing), and was presented twice in a fully intermixed fashion. The subjects' task was to respond manually only to a (rare) pre-specified target stimulus. The nontarget stimuli (the events of interest) were therefore unconfounded by any response requirement, and, more importantly, the dimensions of interest - repetition and familiarity - were incidental to task performance (see Rugg & Doyle, 1994).¹

Bilateral fusiform regions were strongly activated by presentation of both faces and symbols, and moreso for familiar than unfamiliar faces and symbols (suggesting a general role for these regions in visual object recognition, e.g., Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). Furthermore, the right fusiform showed an interaction between repetition effects and stimulus familiarity. Repetition of familiar stimuli was associated with a reduced response, a repetition suppression effect consistent with previous imaging studies (which have generally used familiar stimuli), whereas repetition

of unfamiliar stimuli was associated with an increased response (a “repetition enhancement” effect). This finding suggests that the fusiform regions associated with visual object recognition exhibit dissociable effects of repeating stimuli with, or without, pre-existing representations.

This differential effect of familiarity on repetition-related haemodynamic responses might be taken as consistent with abstractionist theories of repetition priming. Indeed, the repetition suppression for familiar stimuli may reflect more efficient perceptual processing, perhaps owing to reduced thresholds for re-activating abstract representations (a process that could not occur for unfamiliar stimuli). To explain the repetition enhancement for unfamiliar stimuli however, we appealed to a (modified) episodic account based on the perceptual representation theory of Schacter (1990). More specifically, we proposed that 1) the first presentation of an unfamiliar face or symbol was sufficient to form a new perceptual representation, and 2) this representation allowed an additional process of recognition to occur on the second presentation, which was absent on the first. This additional recognition process might then be responsible for the response increase, in the same way that the first presentation of familiar stimuli was associated a greater response in this region than the first presentation of unfamiliar stimuli (i.e., the recognition associated with the basic familiarity effect).²

One advantage of this theory is that it can explain why the only previous functional imaging demonstrations of repetition enhancement have used unfamiliar stimuli, presentation of which was likely to form new perceptual representations. These were 2D drawings of possible (but not impossible) 3D objects (Schacter et al., 1995), or degraded images that were only recognised following prior presentation of an intact

version (Dolan et al., 1997; George et al., 1999). However, our theory remains just one of many possible interpretations of our findings (including, for example, differential effects of attention or explicit memory for familiar and unfamiliar stimuli).

One prediction of our theory is that the interaction between familiarity and repetition will occur in the same regions that are associated with recognition of familiar visual objects. This is in contrast with at least one other explanation of our results, that the right lateralisation of our fusiform repetition effects reflects a right hemispheric specialisation for specific perceptual detail. This episodic-like account is an extension of Marsolek's theory of a general hemispheric specialisation for abstract (*left*) versus specific (*right*) visual-form representations (Marsolek, 1995). This theory is based on data from several split-visual-field behavioural experiments, including, for example, the finding that case changes affect the size of the priming effect in perceptual identification when letter strings are presented to left visual field / right hemisphere, but not the right visual field / left hemisphere (Burgund & Marsolek, 1997). The fact that we found right-lateralised effects for two quite different classes of stimuli, faces and symbols, would appear consistent with this general theory. We felt a stronger test between these theories however would be to use familiar and unfamiliar letter strings, i.e., words and nonwords. Given the left-hemisphere specialisation for linguistic stimuli, our theory predicted that the regions showing the familiarity-by-repetition interaction would be left-lateralised (e.g., in fusiform/inferior temporal regions associated with visual word-forms); the extension of Marsolek's theory however would still predict a right-lateralisation of regions showing this interaction.

Here we report a preliminary test of these predictions in a small sample of six subjects. We note however that the Fixed Effects analysis employed, while providing reasonable statistical power, does not allow us to extrapolate the present findings beyond the sample to the population as a whole (for which further experiments are planned).

Methods

Subjects

Six right-handed volunteers (2 male; aged between 21 and 33) gave informed consent to participate in the experiment. All volunteers reported themselves to be in good health with no history of neurological illness.

Experimental Procedure

Sixty-four five-letter, 1-2 syllable nouns with a Kucera-Francis written frequency of 10-100 were selected from the (MRC Psycholinguistics Database http://www.psy.uwa.edu.au/uwa_mrc.htm). One or more of the letters of a random 32 of these were changed to create pronounceable 1-2 syllable nonwords. Two presentations of each word and each nonword were randomly intermixed, together with 22 five-digit strings (Figure 1). Each stimulus was presented in a 48 pt Helvetica font, white-on-black, on a screen 30cm above the participant, subtending a visual angle of approximately 4 degrees. Stimuli were displayed for 1s, with a random SOA between 6-10s. Subjects were instructed to press a key with their right index finger only when they saw the target digit-string.

Scanning Parameters

A 2T VISION system (Siemens, Erlangen, Germany) was used to acquire T2*-weighted transverse echoplanar images (EPI) of 46 axial slices (64x64 3x3mm² pixels,

TE=40ms) with blood oxygenation level dependent (BOLD) contrast. The 2mm-thick slices were positioned every 3mm, acquired sequentially in a descending direction and continuously during a 20min session. A total of 305 volumes were collected with an effective repetition time (TR) of 4.2s/volume. The first 5 volumes were discarded to allow for T1 equilibration effects. The random jitter in the SOA ensured an effective sampling rate of the impulse response over trials of TR/4 (~1Hz).

Data Analysis

Data were analysed using Statistical Parametric Mapping (SPM99, Wellcome Department of Cognitive Neurology, London, UK; Friston et al., 1995). All volumes were realigned spatially to the first volume and normalised to a standard EPI template based on the MNI reference brain (Ashburner & Friston, 1999) in Talairach space (Talairach & Tournoux, 1988). No subject moved more than ± 2 mm in any direction. The normalised images were smoothed with an isotropic 8mm FWHM Gaussian kernel. Treating the volumes as a timeseries, the data were highpass-filtered to 1/60 Hz and lowpass smoothed with a 4s Gaussian filter (Friston et al., 2000).

The BOLD response to events of the five types (first and second presentation of words and nonwords, plus the targets) were modelled with a Finite Impulse Response basis set of 12 peristimulus time bins of 2s duration. (Once smoothed with the lowpass filter, these basis functions become a series of near-Gaussians staggered by 2s). This general basis set can capture any shape of the impulse BOLD response (up to the frequency limit imposed by the bin size and smoothing). These functions comprised the covariates in a Fixed Effects general linear model (GLM), together with six movement

parameters (the 3 translations and 3 rotations from the realignment), to remove any residual movement-related artifacts, and a constant term, for each session.

Contrasts were performed on the mean parameter estimates across bins 2-4 (i.e., from 2-8s post-stimulus). This allowed a reasonable window during which the peak BOLD response was likely to occur, which was also important given the differences in the relative timing of each slice acquired (because of the long TR, any temporal interpolation of the timeseries in each slice would be likely to alias frequencies close to those in the signal engendered by our SOA; Henson, Buechel, Josephs, & Friston, 1999). Three one-tailed, planned t-tests were performed to identify regions showing: 1) the interaction between word-type (words/nonwords) and repetition (first/second presentation), with relatively greater repetition suppression effect for words than nonwords, 2) greater response to words than nonwords, and 3) greater response to nonwords than words (the latter averaged across presentations). The main effect of repetition (first versus second presentations) was not examined because it is confounded by time in the present design. Resulting SPMs of the t-statistic were thresholded at $p < .001$, uncorrected for multiple comparisons. The maxima of activations were checked on a mean normalised EPI, localised as best as possible on a normalised canonical structural image, and labelled using approximations to the systems of Talairach and Tournoux (1988) and Brodmann (1909) for consistency with previous studies.

Results

The only regions showing the predicted interaction between repetition and word-type were in left anterior fusiform and right posterior parietal cortices (Figure 2). The fusiform region (BA 20; $x = -36$, $y = -6$, $z = -33$; $Z = 3.15$; Figure 2A) showed repetition

suppression for words and repetition enhancement for nonwords (both effects significant at $p < .05$). Furthermore, this region showed a greater response to words than nonwords on their first presentation ($p < .001$). The parietal region, in right intraparietal sulcus (BA 7/40; $x = +36$, $y = -54$, $z = +36$, $Z = 3.71$; Figure 2B) showed significant repetition enhancement for nonwords ($p < .001$), though no evidence of repetition suppression for words ($p > .05$).

The fitted responses from the right midfusiform maximum identified in our previous combined analysis of faces and symbols (BA 37; $x = +48$; $y = -51$; $z = -24$) are also shown in Figure 2A. Though this region showed some evidence of a greater response to words than nonwords ($p < .01$), it failed to show any interaction between word-type and repetition ($p > .05$), unlike the analogous interaction between repetition and familiarity in our previous study (Henson et al., 2000). This supports our contention that the effect of familiarity on repetition-related responses can occur in different brain regions for different types of stimuli.

Finally, we extended our analysis to look for regions showing a main effect of word-type (Table 1). Regions showing greater responses to words than nonwords were found in bilateral inferior parietal cortex (posterior ascending segment of the lateral fissure), right posterior inferior temporal sulcus, and right posterior inferior frontal cortex (pars orbitalis). Regions showing greater responses to nonwords than words were found in left premotor cortex (posterior extent of inferior frontal sulcus), left inferior parietal cortex (deep in anterior intraparietal sulcus), underside of left posterior inferior temporal gyrus, bilateral cuneus (lateral aspects of calcarine sulci), and two regions in left lateral

occipital cortex (most likely in transverse occipital and inferior occipital sulci). There was no evidence for repetition effects in these regions (Figure 3).

Discussion

Having previously shown an interaction between familiarity and repetition in the right fusiform response to both faces and symbols (Henson et al., 2000), we wondered whether this interaction would generalise to a third class of stimuli: familiar and unfamiliar letter strings, i.e., words and nonwords. This generalisation might be expected by Marsolek's theory of a left/right hemispheric specialisation for abstract/specific information respectively (Marsolek, 1995). Namely, the repetition effects in right fusiform cortex, particularly for unfamiliar stimuli with no pre-existing unitary representations (such as nonwords), might reflect the rapid formation of form-specific (episodic) visual representations. This generalisation across stimuli would not necessarily be expected by our theory however, which predicts that the familiarity-by-repetition interaction will be observed in regions that are themselves associated with recognition of familiar stimuli; regions that are likely to differ for different classes of stimuli, particularly linguistic versus nonlinguistic stimuli.

The present results must be regarded as exploratory, given the Fixed Effects analysis of a small subject sample and the uncorrected statistical thresholds. Nonetheless, they tend to favour our theory over the hemispheric specialisation theory. With words and nonwords, the right fusiform region previously identified did not show any repetition effects. A region in the left fusiform however (considerably more anterior than the right fusiform region) showed differential repetition effects for words and nonwords, with repetition suppression for words, but repetition enhancement for nonwords. According to

our theory, the former effect reflects some modification of existing abstract representations (e.g., visual word-forms), whereas the latter reflects the rapid formation of new representations (a process of familiarisation). These new representations allow recognition of the same stimulus when it is presented again (at least as having been seen before). Importantly, this region also showed a greater response to the first presentation of words than first presentation of nonwords, supporting a role in recognition of familiar letter strings. This role is consistent at least with previous findings of a relatively greater response in left anterior fusiform regions during pronunciation of words than of pseudowords (Herbster, Mintun, Nebes, & Becker, 1997; Rumsey et al., 1997; though see below).

We have tended to focus on inferior temporal and fusiform cortices because of their hypothesised role in visual object processing (Mishkin, Ungerleider, & Macko, 1983). Nonetheless, the present, whole-brain study also identified a right intraparietal region that showed an interaction between word-type and repetition, in this case a repetition enhancement for nonwords but little evidence of a repetition effect for words. This pattern may reflect priming at a different level of linguistic processing (e.g., assembly of phonological forms for the visual input). We offer no further explanation for this particular pattern of responses in this particular region however.

Nonetheless, the present experiment also illustrates the inadequacy of our simplistic theory of repetition effects for familiar and unfamiliar stimuli. Familiarity can often be defined at many different levels, particularly for linguistic stimuli. Words for example may have separate orthographic, phonological, lexical and semantic representation in the brain. Conversely, though nonwords are unfamiliar strings of letters,

they may contain familiar sublexical letter sequences or phonological units. This potential multiplicity of different representations concords with the multiple brain regions showing differential responses to words and nonwords in the present study. Thus the differential repetition effects observed for words and nonwords, which we have discussed above in terms of visual word-forms, may instead reflect differences at some other level of representation. For example, the left anterior fusiform region identified here has also been associated with semantic processing, showing effects of semantic/contextual priming of words (Nobre & McCarthy, 1995) and of viewing meaningful versus nonsense objects (Moore & Price, 1999; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996). Thus the present repetition effects may not reflect modification or creation of visual word-forms, but rather changes in semantic processing (though it is unclear how to interpret the repetition enhancement for nonwords, given that simple presentation of nonwords seems unlikely to create new semantic representations).

Resolution of the type of representations/processes from which these repetition effects arise is likely to require more careful control of stimuli; ideally stimuli for which familiarity can be confined to one dimension. Our previous use of faces and symbols is slightly clearer in this sense, though even then, the repetition effects could be attributed to naming of the famous faces and the meaningful symbols, rather than simple visual recognition. One final puzzle is why the differential repetition effects for the symbols were observed in the same right fusiform region as for the faces in our previous study (or at least, in regions that we could not distinguish given the spatial resolution of the data). Symbols would certainly appear more similar to words than to faces, or at least likely to be processed by parts of the language system. Again, we can offer no satisfactory

explanation here, though the answer may be related to the componential aspect of words/nonwords (e.g., consisting of familiar sublexical units), which was absent for our meaningful/meaningless symbols.

Finally, we reiterate that there are several other possible interpretations of the present repetition effects. The different repetition-related responses might reflect differential contributions of explicit memory for example (though explicit memory has been associated with response increases in visual regions, Reber et al., 1998, and yet explicit memory is likely to be better for words than for nonwords). Alternatively, the different repetition-related responses might reflect different degrees of attentional modulation (though the present target detection task does not require differential attention to words and nonwords, and an attentional account is only satisfactory when it explains *why* visual attention differs for first and second presentation of words and nonwords). Questions like these require further experiments, directly manipulating explicit memory and/or attention for example. Indeed, we have preliminary evidence that fusiform repetition effects are not automatic in the sense that they are not task independent (Henson, Shallice, & Dolan, in prep). Nonetheless, though much remains to be done, we believe that repetition priming is a fruitful domain in which psychological, neurophysiological and neuroimaging data can be inter-related, and are already beginning to inform each other.

Endnotes

1. A disadvantage of this task however is the absence of a concurrent behavioural measure of priming (see Henson et al., in prep).
2. We refer here to visual object recognition, rather than “episodic” or “semantic” recognition; the assumption is that both episodic recognition (e.g., “I saw that face before”) and semantic recognition (e.g., “That is Marilyn Monroe”) require an earlier stage of visual object recognition.

- Ashburner, J. & Friston, K. J. (1999). Nonlinear spatial normalization using basis functions. Human Brain Mapping, *7*, 254-266.
- Bowers, J. S. (2000). In defense of abstractionist theories of repetition priming and word identification. Psychon Bull Rev, *7*(1), 83-99.
- Brodmann, K. (1909). Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien dargestellt auf Grund des Zellesbaues. Leipzig: Barth.
- Bruce, V., & Young, A. W. (1986). Understanding face recognition. British Journal of Psychology, *77*, 305-327.
- Burgund, E. D., & Marsolek, C. J. (1997). Letter-case-specific priming in the right cerebral hemisphere with a form-specific perceptual identification task. Brain Cogn, *35*(2), 239-58.
- Desimone, R. (1996). Neural mechanisms for visual memory and their role in attention. P.N.A.S, *93*, 13494-13499.
- Dolan, R. J., Fink, G. R., Rolls, E., Booth, M., Frackowiak, R. S. J., & Friston, K. J. (1997). How the brain learns to see objects and faces in an impoverished context. Nature, *389*, 596-599.
- Ellis, A. W., Young, A. W., & Flude, B. M. (1990). Repetition priming and face processing: priming occurs within the system that responds to the identity of a face. Quarterly Journal of Experimental Psychology, *42A*, 495-512.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J. B., Frith, C. D., & Frackowiak, R. S. J. (1995). Statistical parametric maps in functional imaging; a general linear approach. Human Brain Mapping, *2*, 189-210.

Friston, K. J., Josephs, O., Zarahn, E., Holmes, A. P., Rouquette, S., & Poline, J. (2000). To smooth or not to smooth? Bias and efficiency in fMRI time-series analysis. Neuroimage, 12(2), 196-208.

Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999). Activation of the middle fusiform 'face area' increases with expertise in recognizing novel objects. Nature Neuroscience, 2(6), 568-573.

George, N., Dolan, R. J., Fink, G. R., Baylis, G. C., Russell, C., & Driver, J. (1999). Contrast polarity and face recognition in the human fusiform gyrus. Nature Neuroscience, 2, 574-580.

Henson, R., Shallice, T., & Dolan, R. (2000). Neuroimaging evidence for dissociable forms of repetition priming. Science, 287, 1269-72.

Henson, R. N. A., Buechel, C., Josephs, O., & Friston, K. (1999). The slice-timing problem in event-related fMRI. Neuroimage, 9, 125.

Henson, R. N. A., Shallice, T., & Dolan, R. J. (in prep). Fusiform repetition-related BOLD responses are task-sensitive.

Herbster, A. N., Mintun, M. A., Nebes, R. D., & Becker, J. T. (1997). Regional cerebral blood flow during word and nonword reading. Hum Brain Mapp, 5(2), 84-92.

Jacoby, L. L. (1983). Perceptual enhancement: persistent effects of an experience. Journal of Experimental Psychology: Learning, Memory and Cognition, 9, 21-38.

Marsolek, C. J. (1995). Abstract visual-form representations in the left cerebral hemisphere. J Exp Psychol Hum Percept Perform, 21(2), 375-86.

Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: two cortical pathways. Trends in Neuroscience, 6, 414-417.

Moore, C. J., & Price, C. J. (1999). Three distinct ventral occipitotemporal regions for reading and object naming. Neuroimage, 10(2), 181-92.

Morton, J. (1969). Interaction of information in word recognition. Psychological Review, 76, 165-178.

Nobre, A. C., & McCarthy, G. (1995). Language-related field potentials in the anterior-medial temporal lobe: II. Effects of word type and semantic priming. J Neurosci, 15(2), 1090-8.

Roediger, H. L. I., & Blaxton, T. A. (1987). Effects of varying modality, surface features, and retention interval on priming in word-fragment completion. Memory & Cognition, 15, 379-388.

Rugg, M. D., & Doyle, M. C. (1994). Event-related potentials and stimulus repetition in direct and indirect tests of memory. In H. J. Heinze, T. Munte, & G. R. Mangun (Eds.), Cognitive Electrophysiology (pp. 124-148). Boston: Birkhauser.

Rumsey, J. M., Horwitz, B., Donohue, B. C., Nace, K., Maisog, J. M., & Andreason, P. (1997). Phonological and orthographic components of word recognition. A PET-rCBF study. Brain, 120(Pt 5), 739-59.

- Schacter, D. L. (1990). Perceptual representation systems and implicit memory. Annals of the New York Academy of Sciences, 608, 543-567.
- Schacter, D. L., & Buckner, R. L. (1998). Priming and the brain. Neuron, 20, 185-195.
- Schacter, D. L., Relman, E., Uecker, A., Polster, M. R., Yun, L. S., & Cooper, L. A. (1995). Brain regions associated with retrieval of structurally coherent visual information. Nature, 376, 587-590.
- Stark, C. E., & McClelland, J. L. (2000). Repetition priming of words, pseudowords, and nonwords [In Process Citation]. J Exp Psychol Learn Mem Cogn, 26(4), 945-72.
- Talairach, J., & Tournoux, P. (1988). Co-Planar Stereotaxic Atlas of the Human Brain. Stuttgart: George Thieme Verlag.
- Tenpenny, P. L. (1995). Abstractionist versus episodic theories of repetition priming and word identification. Psychological Bulletin & Review, 2, 339-363.
- Vandenberghe, R., Price, C., Wise, R., Josephs, O., & Frackowiak, R. S. J. (1996). Functional anatomy of a common semantic system for words and pictures. Nature, 383, 254-256.
- Warren, C., & Morton, J. (1982). The effects of priming on picture recognition. British Journal of Psychology, 73, 117-130.

Table 1

Maxima within regions of at least 5 voxels showing word-nonword differences at $p < .001$ uncorrected (L=left, R=right, B=bilateral).

Region of activation	Left /	Brodmann area (BA)	Talairach coords			Z value
	Right		x	y	z	
A. Words > Nonwords						
Inferior frontal	R	45/47	57	21	0	3.21
Inferior parietal	L	40	-57	-42	30	3.33
	R	40	60	-36	30	3.82
Inferior temporal	R	21	51	-48	-3	4.17
B. Nonwords > Words						
Premotor	L	44	-54	6	27	3.52
Intraparietal	L	7/40	-27	-45	45	3.99
Inferior temporal	L	37	-48	-60	-18	4.15
Cuneus	L	17	-24	-69	9	3.77
	R	17	27	-57	9	3.53
Lateral occipital	L	19	-27	-75	27	4.04
	L	18	-36	-90	12	4.08

Figure 1

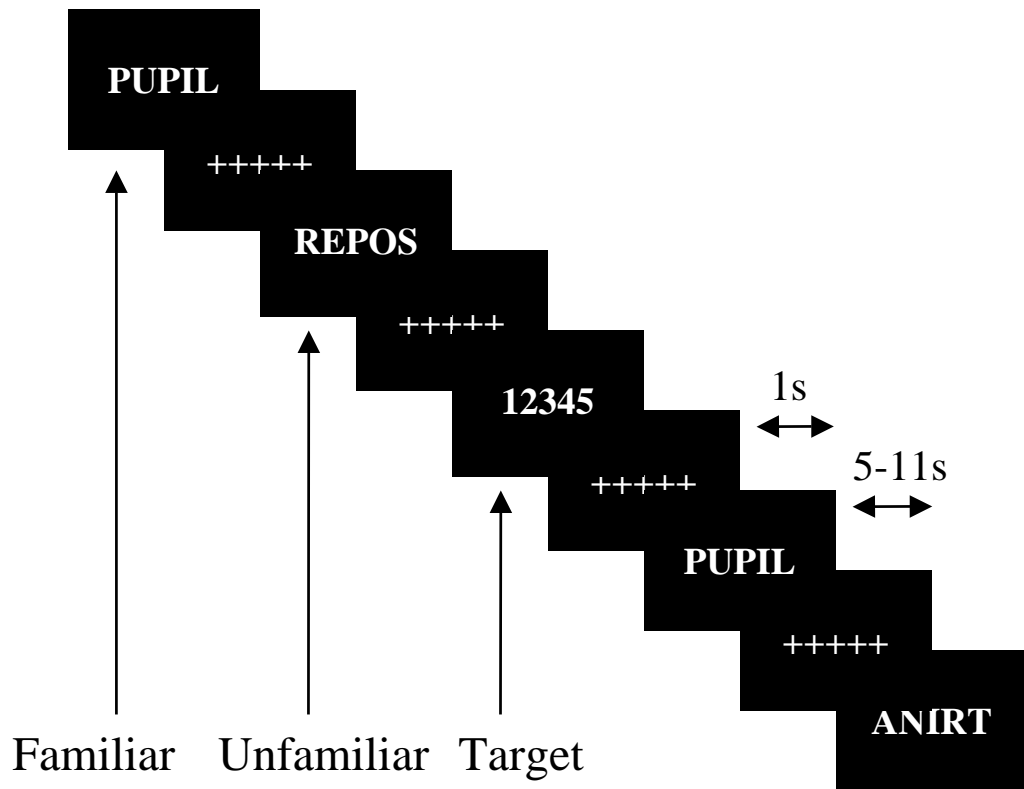
Experimental paradigm: Two presentations of each word or nonword were randomly intermixed with rare targets (digit strings). Participants pressed a key only when they saw a target.

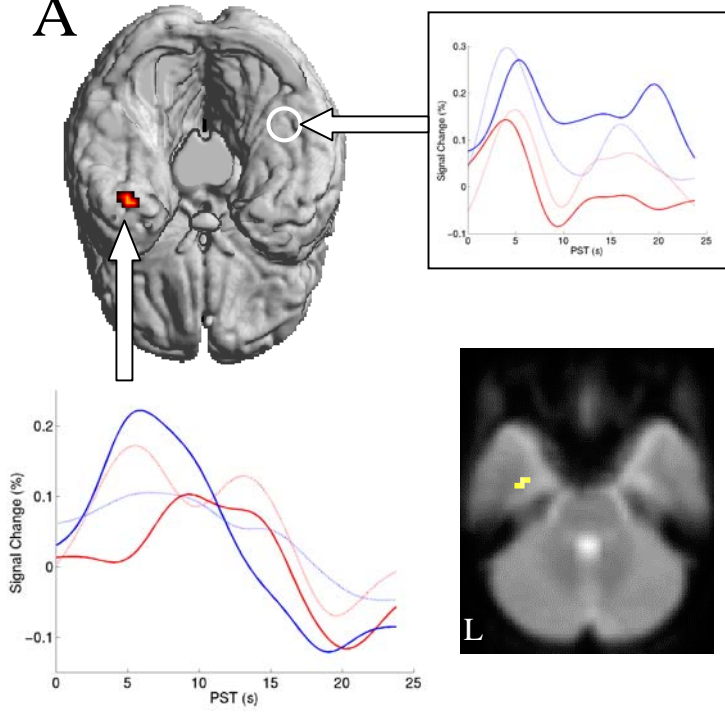
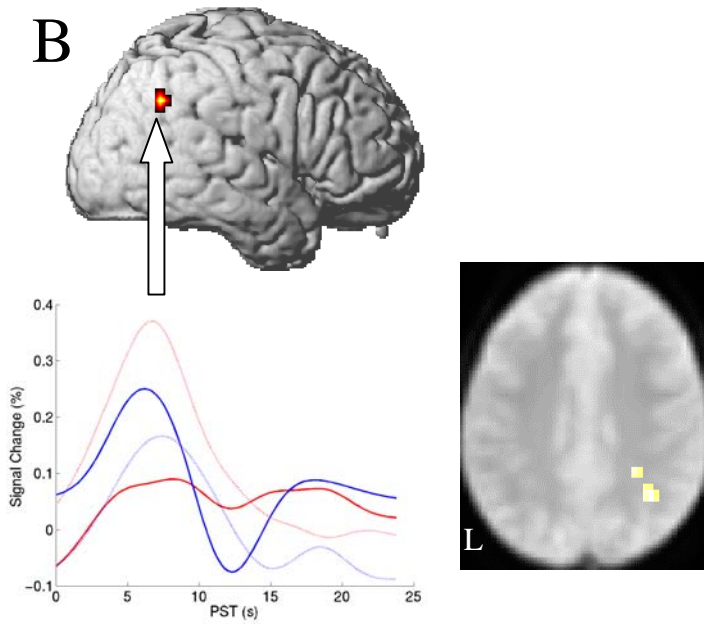
Figure 2

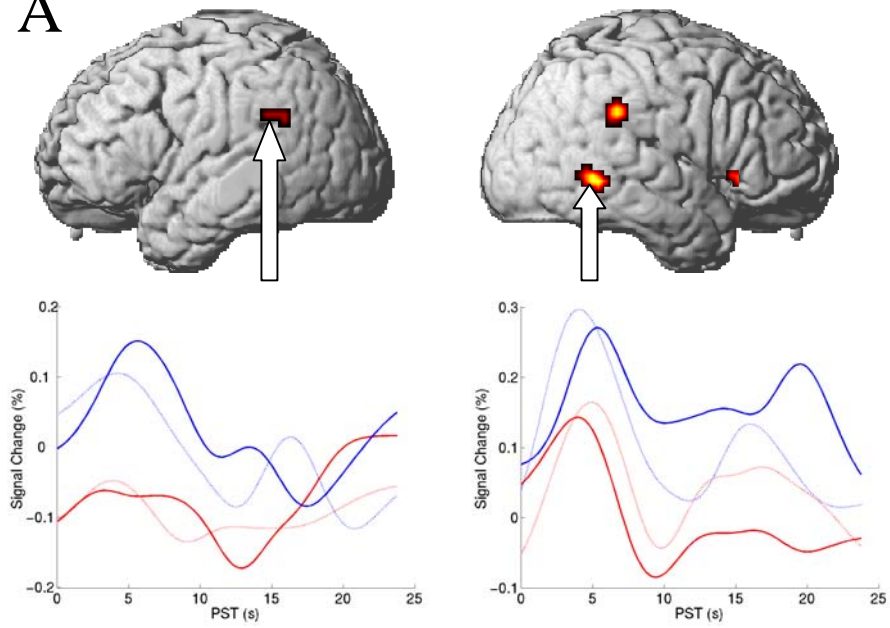
Regions showing differential repetition effects for words and nonwords on (A) the underside and (B) the right lateral surface of the brain. Activations survived $p < .001$ uncorrected (though in panel A, the activation is shown at $p < .005$ for purposes of illustration). The white circle indicates the right fusiform region activated in our previous, but not the current, study. The rendered brain derives from a canonical T1 image with the cerebellum artificially removed, and shows activations within 25mm of surface (note sulcal/gyral anatomy is only approximate). The transverse images derive from a normalised echo-planar image averaged across subjects. The plots show signal change (as percentage of grand mean over voxels and time) for first (solid lines) and second (dotted lines) presentations of words (blue) and nonwords (red) against peristimulus time (PST).

Figure 3

Regions showing greater responses to (A) words than nonwords, and (B) nonwords than words. Activations consisted of at least five voxels surviving $p < .001$ uncorrected. See Figure 2 legend for more details.



A**B**

A**B**