

Research report

fMRI evidence of word frequency and strength effects during episodic memory encoding

Greig I. de Zubicaray^{a,*}, Katie L. McMahon^a, Matthew M. Eastburn^a, Simon Finnigan^a,
Michael S. Humphreys^b

^aCentre for Magnetic Resonance, The University of Queensland, QLD 4072, Australia

^bCentre for Human Factors and Applied Cognitive Psychology, The University of Queensland, QLD, Australia

Accepted 7 October 2004

Available online 28 October 2004

Abstract

Word frequency (WF) and strength effects are two important phenomena associated with episodic memory. The former refers to the superior hit-rate (HR) for low (LF) compared to high frequency (HF) words in recognition memory, while the latter describes the incremental effect(s) upon HRs associated with repeating an item at study. Using the “subsequent memory” method with event-related fMRI, we tested the attention-at-encoding (AE) [M. Glanzer, J.K. Adams, The mirror effect in recognition memory: data and theory, *J. Exp. Psychol.: Learn Mem. Cogn.* 16 (1990) 5–16] explanation of the WF effect. In addition to investigating encoding strength, we addressed if study involves accessing prior representations of repeated items via the same mechanism as that at test [J.L. McClelland, M. Chappell, Familiarity breeds differentiation: a subjective-likelihood approach to the effects of experience in recognition memory, *Psychol. Rev.* 105 (1998) 724–760], entailing recollection [K.J. Malmberg, J.E. Holden, R.M. Shiffrin, Modeling the effects of repetitions, similarity, and normative word frequency on judgments of frequency and recognition memory, *J. Exp. Psychol.: Learn Mem. Cogn.* 30 (2004) 319–331] and whether less processing effort is entailed for encoding each repetition [M. Cary, L.M. Reder, A dual-process account of the list-length and strength-based mirror effects in recognition, *J. Mem. Lang.* 49 (2003) 231–248]. The increased BOLD responses observed in the left inferior prefrontal cortex (LIPC) for the WF effect provide support for an AE account. Less effort does appear to be required for encoding each repetition of an item, as reduced BOLD responses were observed in the LIPC and left lateral temporal cortex; both regions demonstrated increased responses in the conventional subsequent memory analysis. At test, a left lateral parietal BOLD response was observed for studied versus unstudied items, while only medial parietal activity was observed for repeated items at study, indicating that accessing prior representations at encoding does not necessarily occur via the same mechanism as that at test, and is unlikely to involve a conscious recall-like process such as recollection. This information may prove useful for constraining cognitive theories of episodic memory.

© 2004 Elsevier B.V. All rights reserved.

Theme: Neural basis of behaviour

Topic: Cognition

Keywords: Word frequency; Episodic memory; Learning; fMRI; Repetition priming

1. Introduction

Pure single item recognition memory experiments typically involve participants making “old” versus “new” judgements for single words presented at test after they have

studied a word list. Two phenomena identified by these experiments are termed the word frequency (WF) and strength effects, respectively. The WF effect refers to the superior hit-rates (HR; correct “old” responses to studied words) for low frequency (LF) compared to high frequency (HF) words. In addition, for unstudied new words, LF words are less likely than HF words to be judged as old (a “false alarm”)—an example of a mirror effect [28]. The strength

* Corresponding author. Fax: +61 7 3365 3833.

E-mail address: greig.dezubicaray@cmr.uq.edu.au (G.I. de Zubicaray).

effect describes the incremental effect(s) upon HRs associated with repeating an item at encoding [42,65]. Both effects are important phenomena for theories of episodic memory to explain.

Normative word frequencies are utilised in memory experiments as they are assumed to be related to an individual's actual experience of words in everyday life [8]. If this assumption is correct, the WF effect may be related to repetition priming, as Estes and Maddox [19] have suggested. Repetition priming is a well-established effect in which prior exposure to a word facilitates its processing (e.g., the speed with which it can be named or the probability that a degraded version can be identified) at a later presentation [53,59]. According to one encoding-based explanation of the WF effect, HF words attract little attention or processing time when presented in a study list due to their having been already extensively primed, whereas LF words attract more attention due to the relative novelty of their features [28,37,39,41,62]. A corollary to this hypothesis is that the amount of attention allocated to a word at study influences the strength of its episodic memory trace at test. It is known that dividing attention at encoding significantly reduces subsequent memory performance [12]. Alternate explanations of the WF effect place little emphasis on allocation of attention at encoding per se and/or variations in processing during the study phase. For instance, explanations emphasising processes occurring solely at test attribute the LF word HR advantage to the increased noise from the multiple contexts in which HF words have been previously encountered [15], and LF words being recollected more often because of less interference from prior contexts [55].

The attention-at-encoding (AE) account has had limited empirical evidence to directly support it. Behavioural investigations have examined either the amount of self-paced study time allocated to LF and HF words at encoding, or manipulated the presentation duration of study trials (for a review, see Ref. [39]). The former studies have assumed that longer study times are associated with increased allocation of attentional resources; LF words should therefore be studied longer than HF words at encoding. However, this does not provide a direct test of the hypothesis. The latter studies have assumed that limiting the study time permitted during encoding limits the amount of attentional resources that can be allocated; the advantage for LF words should therefore be directly related to study time. Although LF words are typically studied longer than HF words in self-paced experiments, the empirical evidence from the investigations involving experimenter-manipulated study time is mixed [38]. While experiments that confounded study time with study-test lag typically failed to find an effect, experiments using a mixed list design to control for study-test lag have confirmed the AE hypothesis [10,39]. Using the latter design, Malmberg and Nelson [39] showed that the LF word HR advantage was attributable to processing occurring solely between the first 250–1000 ms of study.

It is generally accepted that, as an item is presented repeatedly at study, the stronger its memory trace or signal is at test. Single process models of memory tend to assume the existence of a single, continuous multicomponent memory trace or signal, while dual-process theories consider encoding strength to involve contributions from putatively separate familiarity and recollection-based processes. Although the proposed mechanisms for strengthening a memory trace vary between theories, most assume an incrementing process of sorts. For example, in Shiffrin and Steyvers' [63] "retrieving effectively from memory" (REM) single-process model, this is attributed to the increased processing and storage of item features with each additional presentation. In Malmberg et al.'s [40] dual-process extension of REM, recollection (a recall-like process) serves the purpose of assessing the content of an episodic trace. As content becomes stronger with increasing storage of item features, a better assessment of the features can be provided, assisting correct rejection of unstudied items at test. Repetition is also considered to strengthen both familiarity and recollection in other dual-process theories [55,72].

Some issues associated with encoding strength also warrant mention here: First, study may involve accessing prior representations of repeated items, or assessing their content [40], and where this issue has been explicitly addressed in theory, it has been assumed to involve the same mechanism involved in recognition at test [42]. However, each presentation of an item might also be stored separately [35,51]. Second, a repetition priming effect of sorts occurs with multiple presentations at study as well as at test [53,59].¹ This might indicate that less attentional or processing effort is entailed for encoding each repeated presentation of an item compared to the first, as Cary and Reder [7] have speculated recently. Without this assumption, repeated presentations of items produced identical amounts of memory strengthening in their dual-process model, resulting in a poor fit to experimental data [7].

Cognitive neuroscience investigations of episodic encoding have exploited the "subsequent memory" method. This procedure involves contrasting neural activity measured during study of a series of items according to whether an item is recognised or not at test. Any differences found are assumed to represent successful encoding-related processes (for reviews, see Refs. [57,69]).² Cerebral regions found to

¹ Repetition priming is typically considered an index of implicit or unconscious memory processes. However, with item repetition during encoding, there is the potential for participants to make explicit connections between the separate study events, particularly when several study/test blocks are employed, as is the case here.

² This assumption neglects the fact that several theories assume forgetting processes that would not be revealed by a simple comparison between subsequently remembered and unrecognised items. For example, Murdock and Lamon [44] attributed forgetting to the characteristics of the other items in a study list, while Dennis and Humphreys [15] assume a major role for contextual reinstatement and preexisting associates with context.

be activated consistently during the encoding of single words using this procedure with event-related fMRI include the left inferior and medial areas of the frontal cortex and less reliably so, the medial temporal lobe (MTL [48,47,54]). An explanation for the less consistent finding of MTL activity in subsequent memory studies remains elusive [57]. Aside from the lower signal-to-noise ratio (SNR) observed in the MTL compared to adjacent cortical structures, it has been suggested that the frequent failure to observe MTL activity during the encoding of single items in fMRI experiments might be due to the relative absence of relational processing requirements that presumably engage this area to a greater extent than storage alone [61]. Interpretations of activity differences have tended to ascribe roles of processing an item's semantic and phonological content during encoding to the left inferior prefrontal cortex (LIPC) [16,22,27], and where observed, encoding success or item storage to the MTL [5,54,69]. In addition, the activity in the LIPC appears to be modulated according to the effort involved or allocation of attentional resources during encoding [54,70].

It is important to note that the overwhelming majority of these subsequent memory studies have employed incidental encoding tasks, contrasting alphabetic versus semantic judgements during encoding in order to examine “depth of processing” effects [57,69]. Intentional encoding tasks, in which participants are instructed simply to remember items as they are presented, have been employed only rarely. Conversely, cognitive studies of the WF and strength effects have invariably relied upon an intentional encoding procedure, and the extant theoretical models discussed earlier are based upon this data [28,37,42].

Investigations that have contrasted *retrieval related activity* between studied and unstudied (old/new) items at test have revealed consistent involvement of distinct anterior, dorsal and ventral regions of the prefrontal cortex, the left lateral and medial (cuneus/precuneus) parietal cortex and, less consistently, the MTL [17,18,30]. The respective roles of the different sites of prefrontal activity observed at test continue to be the subject of debate, although some consensus has been achieved regarding the right dorsal region's involvement in the monitoring and evaluation of the products of a retrieval attempt [58]. Left ventral prefrontal cortex may be involved in retrieval success or the outcome of the retrieval attempt [17,58], while the right anterior region (frontal polar cortex) is proposed to be involved in the maintenance of “episodic retrieval mode”, a mental set or state deemed necessary for remembering studied items [36]. Responses in the left hemisphere parietal cortex and hippocampal formation in the MTL (when present) both tend to be interpreted as more directly reflecting processes associated with conscious retrieval attempts, or recollection, although debate continues regarding the precise roles of the medial and lateral parietal cortices [17,18,30,57,71]. In a recent fMRI study, the lateral region of the left parietal cortex (BA 39/40) demonstrated

activity associated with the perception of an item as being old, even if an old response was not correct [71]. Wheeler and Buckner [71] therefore proposed that the level of activity in this region could be used to determine whether previously experienced information was identified or recovered.

In the current study, we employed event-related fMRI and extended the subsequent memory method to contrast cerebral blood oxygen level dependent (BOLD [45]) responses during the successful intentional encoding of LF versus HF words, and first versus repeated presentations. Specifically, we addressed whether the HR advantage for LF words is attributable to greater allocation of attention to their features at encoding [28,37,39,41,62]. If an AE explanation is correct, then LF words should yield greater activity than HF words in the LIPC during encoding, as this area has been associated with processing requirements during word encoding experiments [57,69]. While MTL activity has been linked with successful memory storage or success [54], there is no compelling a priori reason to assume that the amount of attention allocated selectively to unusual word features during encoding will be reflected in changes in MTL activity, although we do not dismiss this possibility as the dual-process theory proposed by Rugg and Yonelinas [56] views recollection (a putative hippocampus-mediated process) as requiring more attention than familiarity during encoding. This view attributes the LF word advantage at test to both recollection and familiarity, with relatively greater involvement of the former process [72]. However, other dual-process models view recollection as not contributing to the LF word HR advantage [40].

A relatively consistent finding in neurophysiological experiments is that novel stimuli elicit increased neural responses compared to repeated items, particularly in the temporal and prefrontal cortices [52]. The reduced responses observed for repeated items have been referred to as “repetition suppression” effects and have been observed in conjunction with behavioural priming in neuroimaging experiments [29,60]. Wagner et al. [70] suggested that, as episodic encoding is considered to reflect attention directed to task-relevant stimulus features, this might result in priming of these features during repeated presentation, thus reducing the demand on attentional operations mediated by the LIPC for encoding. This suggestion provides a plausible candidate area for testing whether less attentional or processing effort is entailed for encoding each repeated presentation of an item compared to the first [7].

Finally, if study involves accessing prior representations of repeated items via the same mechanism as that at test [42], or assessing the content of an episodic trace through recollection [40], then the following cortical areas seem the most likely candidates to demonstrate increased BOLD signals given past results and their interpretations: the left parietal cortex and hippocampal formation in the MTL (but see Ref. [61]) [17,18,30,57,71]. In particular, if lateral parietal cortex activity is an index of whether an

item is identified or recovered at test [71], then this region should show responses with item repetition at study if the same neural mechanism underlies both effects, or if item content is assessed through recollection at a conscious level.

2. Materials and methods

2.1. Participants

Fourteen healthy adult volunteers (seven female) were recruited to perform the study (mean age 28.6 years, range 21–38) and were reimbursed AUD\$30 for their participation. All volunteers were right handed, native speakers of English, with no history of neurological or psychiatric disorders. Informed consent in writing was obtained prior to the experiment, with procedures approved by the University of Queensland's Medical Research Ethics Committee.

2.2. Task and procedure

The experiment involved three consecutive study/test sessions conducted within the bore of the MRI scanner, with a brief rest break (1–2 min) between sessions. During the study phase of each session, 12 LF and 12 HF words were presented once, and 12 LF and 12 HF words were presented twice. Each study list therefore consisted of a total of 72 word presentations, of which 48 were unique words (24 per frequency condition). All words were presented for 800 ms with an interval between presentations of 2200 ms during which participants viewed a blank screen. A fixed stimulus duration of 800 ms was chosen as Malmberg and Nelson [39] showed that the LF word HR advantage is attributable to study occurring solely between the first 250 and 1000 ms. Participants were instructed to memorise the words for an immediate, episodic recognition test.

Following each study list, a test list was presented. At test, new (i.e., unstudied) and old (first and second presentation) words were presented one at a time, and subjects made an old/new judgment for each test word. Test lists consisted of 12 LF and 12 HF first presentation words, 12 LF and 12 HF second presentation words, plus 12 LF and 12 HF new words. Therefore, the total length of each test list was 72 words. The order of presentation was randomly intermixed among the six conditions. In order to minimise study-test repetition lag variability, all studied words were presented in the same third of the test list as at study. For each single trial/word a centrally placed fixation point (a "+") appeared initially for 600 ms, which was then followed by a blank screen for 200 ms and the word for 2500 ms. Participants were instructed to withhold their response during this period (i.e. until the word disappeared from the screen). Next, the words "old" and "new" were presented together, side by side for up to 2000 ms. This

served both as a prompt to respond, and to indicate which button should be pressed for a given response. Participants' placed their left and right index fingers above one of two response buttons throughout the test phase and responded by pressing the button corresponding to their "old" or "new" judgment. The word "old" or "new" changed colour to red for 200 ms to provide response feedback and a fixation point was presented for the remainder of the 2000-ms period. The response position was counterbalanced such that "old" appeared on the left side and "new" on the right in 50% of trials, and was varied randomly from trial to trial.

Prior to scanning, participants completed a brief practice session involving three words each of first and second presentation LF and HF words at study, followed by a test list comprising these words and three new HF and LF words.

Word lists: All words were five letters in length. Equal numbers of low (1–4 occurrences per million) and high frequency (50–100 per million) words were selected from "The Sydney Morning Herald" word database of Australian English [14]. The practice and each study/test session consisted of different words: None were repeated across lists.

2.3. Apparatus

A laptop PC running Microsoft VisualBasic and Exact-Ticks (Ryle Design) software was used to deliver the word stimuli and record responses from an MR-compatible dual button box. Stimuli were presented in black on a luminous white background, enlarged and back-projected using a BenQ SL705X projector onto a screen, which the participants viewed through a mirror mounted on the head coil. The stimuli subtended approximately 10° of visual arc when each participant was positioned for imaging.

2.4. Image acquisition

Participants were imaged with a 1.5-T Siemens Sonata system using a standard circularly polarised head coil for RF reception. A gradient echo planar imaging (EPI) sequence was used to acquire T2*-weighted images depicting BOLD contrast (64×64 matrix, 3.75×3.75 mm voxels). In each of 3 consecutive acquisitions, 300 whole-brain volumes consisting of 21 near axial 5 mm slices (0.5 mm gap) were acquired continuously in an interleaved series (repetition time, 2100 ms; echo time, 40 ms; flip angle, 90°), giving an effective slice acquisition time of 100 ms. The first five volumes from each acquisition were discarded in order to allow for steady-state tissue magnetisation to be achieved. Head movement was limited by foam inserts within the head coil. In the same session, a high-resolution 3D T1-weighted image (256³ matrix, 0.9 mm³ voxels) was acquired using a magnetisation prepared rapid acquisition gradient echo (MP-RAGE) sequence.

2.5. fMRI data analysis

Image pre-processing and statistical analyses were carried out using statistical parametric mapping software (SPM2; Wellcome Department of Cognitive Neurology, Queens Square, London, UK). Time-series volumes from the three sessions were resampled using generalised interpolation to the acquisition of the middle slice in time to correct for the interleaved acquisition sequence [66], then realigned to the first volume of the initial session using a set of six rigid-body transformation parameters and variance attributable to movement-by-susceptibility interactions removed (“realign and unwarp” option [1,24]). A mean image was generated from this data, which was then spatially normalised via non-linear basis functions to the corresponding SPM2 EPI template image in MNI atlas space [2,20]. The non-linear transformations were next applied to the time-series volumes from which the mean had been generated. Normalised volumes were then resampled to 3 mm³ voxels and convolved with an 8-mm full width half maximum (FWHM) isotropic Gaussian kernel.

Statistical analysis of the fMRI data from the study and test lists was conducted in two stages of a mixed effects model using classical inference [26]. The BOLD responses to hits (correct “old” responses to studied words) and misses (incorrect “new” responses to studied words) from each study condition and presentation (first and second presentation LF and HF words) were modelled with delta (“stick”) functions representing each presentation onset, and convolved with a synthetic hemodynamic response function (HRF) and its temporal and dispersion derivatives [25]. The BOLD responses to hits, misses, false alarms (FA; incorrect “old” responses to unstudied words) and correct rejections (CR; “new” responses to unstudied words) from each test condition and presentation (first and second presentation and new LF and HF words) were also modelled in a similar manner. The resulting functions were high-pass filtered to 1/128 Hz to remove low-frequency noise, and linear contrasts of the parameter estimates of the HRF from each participant were used in the second-stage analyses that treated participants as a random effect. These consisted of one-sample *t*-tests across participants for each contrast and the *t*-values were then transformed into corresponding *Z*-scores.

The “subsequent memory” effect [57,60] was determined by comparing, for first presentation words only, hits (from a possible total of 144 words) with misses. In order to identify only those regions where WF and encoding effects coexisted, we compared hits for first presentation LF versus HF words (a possible total of 72 words was available for each frequency condition), and inclusively masked these contrasts with the results of the subsequent memory analysis. This approach substantially reduces the probability of false positives by limiting the number of voxels searched. Comparisons were restricted to first presentation words in order to avoid confounds associated with repeated presentations, including a known weakening of the frequency effect [59]. Hits for LF

and HF words were combined for comparisons of first versus second presentation words to examine the strength effect irrespective of word frequency (a possible total of 72 words in each condition), and again inclusively masked with the results of the subsequent memory analysis.

Following Otten et al. [49], the mask used in the WF and strength analyses did not take into account the direction of the subsequent memory effect, as there is no a priori reason to assume that brain regions influencing memory encoding will show only increases in activity. Masks were generated using an α threshold of 0.005 ($Z > 2.58$, uncorrected). This threshold was chosen in order to permit potential responses in the MTL to be included in the mask, given the lower SNR observed in this region compared to adjacent cortical structures [13,17,61,64].

In order to determine whether study involves accessing prior representations of repeated items via the same mechanism as that at test, or assessing the content of an episodic trace through recollection, we performed two contrasts using the test fMRI data. The first involved comparing hits to all presented studied words versus CRs to unstudied words to identify retrieval related responses (old/new effect). The second provided a direct comparison of the hits to studied words at test versus hits to second presentation words at study. Analyses of the remaining test data will be reported elsewhere.

Effects were considered significant if a region consisted of >8 contiguous voxels and exceeded a one-tailed α threshold of 0.001 ($Z > 3.09$, uncorrected for multiple comparisons) [17,49,58,70]. As there were no a priori predictions concerning BOLD signal increases associated with HF words, a more conservative α threshold of 0.0005 was employed for these comparisons (corresponding to a two-tailed threshold of 0.001) following Otten et al. [49]. As previously stated, the threshold for the MTL was selectively lowered to 0.005, due to the lower SNR observed in this region compared to adjacent cortical structures [13,17,61,64]. Statistical maps of BOLD responses were displayed in atlas space using the Computerised Anatomical Reconstruction and Editing Toolkit (CARET) [68].

3. Results

3.1. Behavioural data

For hit-rates, both word frequency [$F(1,13)=4.34$, $MSE=0.119$, $p < 0.05$] and strength [$F(1,13)=9.41$, $MSE=0.259$, $p < 0.005$] had significant effects. The interaction of word frequency and strength was not significant [$F(1,13)=0.546$, $MSE=0.015$, $p > 0.05$]. Fig. 1 shows the LF word HR advantage for both weak and strong words. The FA rate was significantly greater for HF than for LF words (0.166 versus 0.113, respectively, $t(13)=5.752$, $SEM=0.03$, $p < 0.001$). Thus, a mirror-patterned WF effect was observed overall.

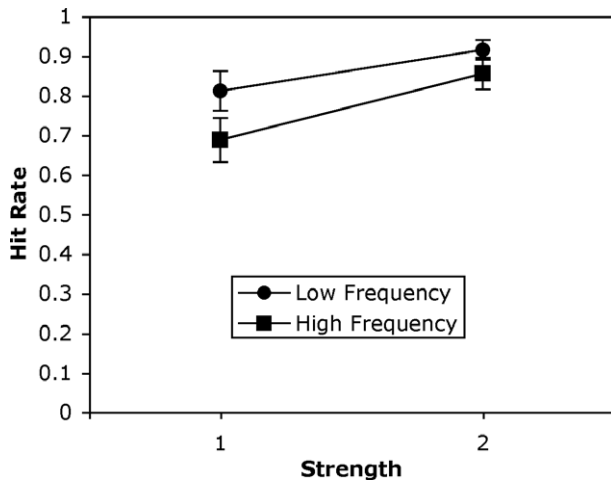


Fig. 1. HRs as a function of word frequency and item repetition (strength) at study. Error bars are standard errors.

3.2. fMRI data

Unless otherwise noted, the α threshold for significantly activated voxels is 0.001 (uncorrected), and x , y and z coordinates are in MNI atlas space.

The first analysis compared encoding-related activity elicited by hits versus misses for first presentation words (Fig. 2a). This subsequent memory analysis demonstrated significant left frontal cortical activation, located in the

ventral and dorsal inferior frontal gyrus ($-45, 27, -12$; $Z=4.51$; BA 47 and $-48, 36, 15$; $Z=4.39$; BA 46, respectively), medial frontal gyrus ($0, 6, 60$; $Z=3.74$; BA 6) and precentral gyrus ($-48, -3, 54$; $Z=4.58$; BA 6). Activation in the middle temporal gyrus ($-51, -45, 6$; $Z=3.51$; BA 22) and fusiform gyrus ($-48, -66, -12$; $Z=3.99$; BA 37) also predicted subsequent memory. No evidence of MTL activity associated with subsequent memory was observed at the lower α threshold of 0.005. In order to determine whether a trend toward a subsequent memory effect existed, we adopted a much more lenient threshold of 0.01 (uncorrected) following the practice of previous studies [17,49,47]. Importantly, within the MTL there was no evidence of a trend toward a subsequent memory effect using this very lenient threshold.

The second analysis compared hits for first presentation LF versus hits for HF words (Fig. 2b). In this “word frequency” analysis, only one significant effect was observed in the left inferior PFC, at a slightly lower significance level of $p=0.002$ ($-42, 39, 9$; $Z=2.84$; BA 10). The third analysis tested for responses to hits for second presentation versus first presentation words (Fig. 2c). This “strength” comparison demonstrated significant activation extending through the medial parietal cortex (precuneus), with a focus in the right hemisphere ($3, -78, 42$; $Z=5.34$; BA 7) and right posterior middle temporal cortex ($39, -63, 24$; $Z=4.43$; BA 39).

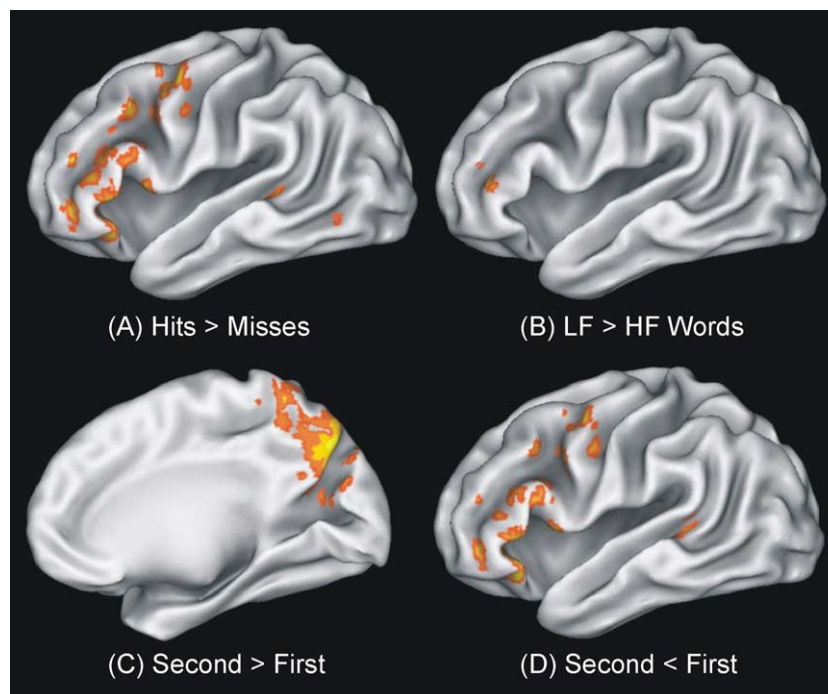


Fig. 2. Inflated views of the cortical regions in which BOLD responses were observed across the group of 14 participants in the mixed-effects analyses (refer to text for coordinates and Z-scores): (A) Lateral view of the left hemisphere regions in which increased responses were observed during the conventional subsequent memory analysis (hits>misses for first presentation words), including the LIPC, lateral middle temporal and occipitotemporal cortices. (B) Lateral view of the LIPC region in which activity was observed for the WF effect (hits to LF>HF first presentation words). (C) Right hemisphere medial view of the parietal region (precuneus) in which activity was observed for the strength effect (hits to second>first presentation words). (D) Left lateral view of the regions in which repetition priming effects were observed, including the LIPC and lateral middle temporal cortex (hits to first>second presentation words).

The fourth analysis involved the reverse comparison (hits for first versus second presentation conditions) and examined the hypothesised repetition priming effect during encoding. This analysis demonstrated significant involvement of the left frontal cortex, especially inferior frontal gyrus ($-45, 24, -9$; $Z=4.54$; BA 47 and $-57, 15, 21$; $Z=3.73$; BA 9), middle ($-48, 0, 51$, $Z=4.27$; BA 6) and medial ($-3, 6, 57$; $Z=3.89$; BA 6) frontal gyri (Fig. 2b). Two of these maxima, located in the inferior and medial frontal gyri (BAs 47 and 6, respectively), shared near-identical peak maxima to those identified in the subsequent memory analysis reported above (compare Fig. 2a and d). Greater responses for first presentation words were also observed in the left middle temporal gyrus ($-51, -45, 6$; $Z=3.70$; BA 22), with a focus identical to one observed in the subsequent memory analysis.

For the test data, the comparison of hits to all presented studied versus unstudied words (old > new effect) revealed increased BOLD responses in the left lateral superior parietal cortex ($-33, -60, 45$; $Z=4.92$; BA 7). A series of left frontal cortical areas also showed increased responses, namely middle ($-42, -3, 54$; $Z=4.42$; BA 6, and $-30, 51, 3$; $Z=3.48$; BA 10, and $-48, 18, 36$; $Z=3.63$; BA 8), inferior ($-48, 45, -3$; $Z=3.72$; BA 10 and $-51, 3, 27$; $Z=3.48$) and medial frontal gyri ($-3, 9, 57$; $Z=4.58$, and $-12, 45, -15$; $Z=3.69$). Additional responses were observed bilaterally in occipital cortex ($33, -90, 6$; $Z=3.76$; BA 18, and $-30, -96, 12$; $Z=3.68$; BA 18) and insula ($-36, 27, -3$; $Z=3.89$, and $33, 21, 3$; $Z=4.24$). A subset of these regions are shown in Fig. 3a. No evidence of a MTL effect for this contrast was observed even at a more lenient α threshold of 0.01.

The final comparison of hits to studied words at test versus hits to second presentation words at study investigated whether the same neural mechanism is involved in accessing prior representations of repeated items in both conditions (test and study), or assessing the content of an episodic trace through recollection. This analysis revealed greater BOLD responses during recognition at test in the left

lateral superior parietal cortex, at a focus similar to that observed for studied versus unstudied items at test ($-30, -63, 57$; $Z=4.12$; BA 7) (compare Fig. 3a and b). Greater responses were also observed bilaterally in frontal cortical areas, including the inferior ($-36, 24, -3$; $Z=3.72$; BA 47, and $33, 24, 3$; $Z=3.68$, BA 45, and $36, 24, -9$; $Z=3.41$), medial ($-12, 51, -15$; $Z=3.68$) and superior ($-3, 9, 57$; $Z=3.76$; BA 6) frontal gyri. Finally, additional responses were observed bilaterally in occipital cortex ($-30, -96, 12$; $Z=3.63$; BA 19, and $24, -102, 3$; $Z=3.76$; BA 18). Again, no evidence of a MTL effect was observed even at a more lenient α threshold of 0.01.

4. Discussion

Word frequency and strength effects are important phenomena for theories of episodic memory to explain. The measurement of these effects ultimately provides constraints for theory development. The fMRI data reported here from an intentional encoding task support an AE explanation of the WF effect [28,37,39,41,62]. The data also show that study might not necessarily involve accessing prior representations of repeated items via the same mechanism as recognition at test [42], nor might it involve a conscious assessment of the content of an episodic trace through recollection [40]. However, less attention or processing effort does appear to be required for encoding each repeated item presentation [7]. This information may prove useful for constraining cognitive theories of episodic memory effects, as we discuss below.

4.1. The attention-at-encoding account of the WF effect

Despite having been proposed nearly two decades ago, the AE explanation for the WF effect in recognition memory as originally formulated has had limited empirical evidence to directly support it [28,39]. An alternative AE explanation

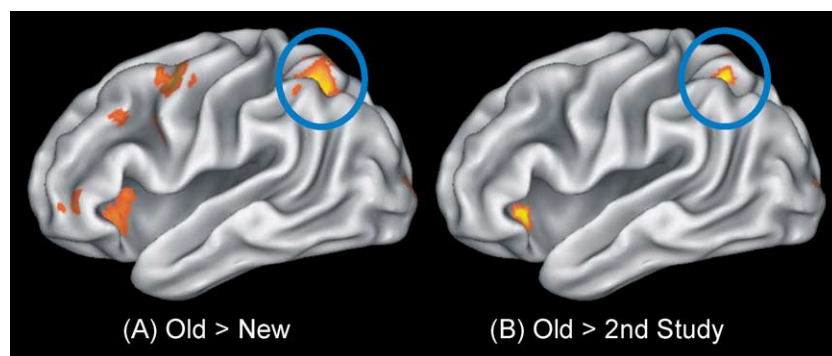


Fig. 3. Inflated views of some of the cortical regions in which BOLD responses were observed across the group of 14 participants in the mixed-effects analyses (refer to text for coordinates and Z-scores): (A) Left hemisphere lateral view of the regions that demonstrated increased BOLD responses for the old/new effect (correct studied > unstudied items at test). The lateral parietal cortex response is circled. (B) Left lateral view of the regions that demonstrated increased BOLD responses for the comparison of correct studied (old) items at test versus hits to second presentation words at study. The lateral parietal cortex response is circled.

has been implemented recently in a formal computational framework in an extension of the REM model [38]. According to this account, some features are “marked” when words are studied and marking is directly related to the amount of attention an item receives at encoding [28,38]. Relatively more features of HF words are assumed to be marked prior to study, due to their having been encountered more often in everyday use. The WF effect is assumed to occur because LF words attract more attention than HF words due to their relative novelty, and therefore have more of their features marked at study. The significant LF word HR advantage and relatively greater BOLD response in the LIPC in the present study support this AE explanation. The LIPC has demonstrated activity consistently during verbal encoding and lexical processing of LF versus HF words in previous neuroimaging studies [9,49,57], and is therefore a physiologically plausible area for mediating the proposed increased attentional demands of processing LF words.

Based upon their finding that the LF word HR advantage did not increase with study beyond 1 s, Malmberg and Nelson [39] recently proposed a revised version of the AE account in which the increased attentional allocation to LF words occurs during an early rather than late phase of studying while the orthographic, graphemic and/or phonological features of a word are processed. During the late phase, controlled processing of semantic features occurs that is dedicated to encoding the word into long-term memory, although this is not considered to contribute to the LF word HR advantage (i.e., semantic processing is considered equivalent for both HF and LF words) [39]. Although we did not directly manipulate attention by limiting the amount of time permitted for study to early (<1 s) versus late (>1 s) phases, our word stimuli were presented for 800 ms, which is within the time period identified by Malmberg and Nelson [39] as being responsible for the WF effect in encoding. For this reason, we infer that the observed LIPC response more likely reflects the relatively greater allocation of attention selectively to the novel features of LF words compared to those of HF words during intentional encoding, rather than semantic processing per se, which has been suggested as another possible role for the LIPC based upon neuroimaging data from lexical decision (word/non-word), incidental encoding and reading tasks [9,21,23], although we acknowledge the latter explanation cannot be excluded. Future experiments that directly contrast cerebral activity during early versus late phases of encoding may shed further light upon this issue.

It is important to note that even though an AE explanation is largely supported by the fMRI data, this result does not necessarily preclude additional mechanisms that possibly contribute to the WF effect at test, including the increased context noise associated with HF words [15], or the more “diagnostic” or distinctive features of LF words, as proposed by the REM model [63] and its extensions [40,38].

4.2. Encoding strength

Recognition was superior for items that received repeated presentation than for items that received only a single presentation at study—the encoding strength effect [7,42,65]. Virtually, all single- and dual-process memory theories assume an incrementing process of sorts to underlie the strength effect. In addition to investigating encoding strength, we examined some issues proposed to be related to this effect: Whether study involves accessing prior representations of repeated items via the same mechanism as that at test [42], or similarly, assessing the content of an episodic trace through recollection [40], and whether the repetition priming effect associated with repeated presentation at study [59] occurs because less attentional or processing effort is entailed for encoding each repeated presentation [7].

As our primary concern here is with item repetition at encoding, we will confine our discussion of the analyses of the test data to the left lateral and medial parietal cortices, as these regions have been implicated previously in episodic retrieval success and are the most relevant to our hypotheses concerning the strength effect (see Introduction) [17,30,57]. Of the two subregions of the parietal cortex, the lateral area has received the greater emphasis in terms of its role in retrieval success, despite both lateral and medial regions often demonstrating equivalent responses [17]. Recently, Wheeler and Buckner [71] reported that the lateral region (BA 39/40) demonstrated activity associated with the perception of an item as being old, even if an old response was not correct. They suggested that the implication of this result was that the level of activity in lateral parietal cortex could be used to predict whether previously experienced information was identified or recovered. In the present study, increased BOLD responses for repeated items at encoding were observed extending throughout the medial parietal cortex, consistent with previous studies of item repetition effects in continuous recognition [33]. This pattern of responses differed from the Old/New effect in recognition at test in which left lateral parietal cortex activity was observed.

If lateral parietal cortex is more directly associated with the identification or recovery of previously studied information [71], then the absence of a response in this area for repeated words indicates that it is unlikely that study involves accessing prior representations of repeated items via the same mechanism as that at test [42]. Similarly, if an item is not explicitly identified as old during repetition at study, it seems reasonable to assume that its content is not being assessed consciously (i.e., recollected), contrary to the assumption of the dual-process extension of the REM model proposed by Malmberg et al. [40]. This is perhaps not surprising, given that the demand characteristics of an explicit retrieval task involving making an old/new judgement differ considerably from the unintentional or implicit retrieval occurring during study, no doubt resulting in the lateral parietal cortex being engaged less often for second presentation items during encoding than for old items during

retrieval. There is also the possibility that each presentation of an item is stored separately, as Landauer [35] proposed. Similarly, Raaijmakers [51] has recently proposed a model in which the episodic memory image of an item is not necessarily retrieved on its second presentation. If it is not retrieved, a new image is stored instead.

This leaves the question of the role of the medial parietal cortex in episodic memory. Cabeza et al. [6] reported that activity in this region appeared common to both episodic retrieval and visual attention-based tasks, and that it might therefore be involved in orienting attention to internally generated stimuli. This interpretation appears consistent with the notion that some items are not remembered because they fail to receive enough attention at encoding [12]. Does this mean that the medial parietal cortex response observed for repeated items at study is an index of sorts of the amount of attention retained by an item's representation at encoding? We suggest that this is the case, and that it might also be characterised consequently as reflecting the strength of an episodic trace. Note this interpretation is qualitatively different to the role proposed for the LIPC in *directing* attention selectively to task-relevant stimulus features during encoding considered responsible for the WF effect [70].

Repetition priming effects have been associated reliably with reductions in cerebral hemodynamic responses in neuroimaging studies [29,60]. The physiological mechanism underlying these responses is thought to be the reduced firing of neurons following repetition of a stimulus [4,29,52]. Reduced BOLD responses for second presentation words were observed in the LIPC and medial frontal cortex in foci identical or near-identical to those identified in the conventional subsequent memory analysis. Findings of LIPC and medial frontal cortical responses during verbal encoding have been replicated consistently [47,54,57]. The LIPC activity has in particular been attributed to the effort involved in processing a word's semantic and/or phonological content during encoding [5,54,69,70]. In their study of priming during incidental encoding, Wagner et al. [70] found reduced LIPC activation for items that had been presented prior to scanning relative to new items. In the context of these results, the present data support the suggestion that less attentional or processing effort is entailed for encoding each repeated presentation of an item compared to the first [7].

Middle temporal cortex responses have likewise been reported in subsequent memory studies [54] and directly during electrophysiological recordings of word encoding [46]. The left middle temporal focus that demonstrated a reduced response for repeated words was nearly identical to the focus identified in the subsequent memory analysis. Reduced left middle temporal BOLD responses have been observed in fMRI studies of semantic priming and attributed to semantic processing [11,29], while Thompson-Schill et al. [67] proposed a role for this region in the storage and retrieval of word concepts. Either process could be

considered consistent with the present result, i.e., relatively less semantic information is stored at repeated presentation, or accessing semantic information established at initial presentation is relatively facilitated [11]. This is again consistent with the suggestion that less processing effort is entailed for encoding repeated presentations of items.

4.3. The MTL and episodic memory

Activity in the MTL has not been observed consistently in neuroimaging studies of episodic memory [57], and we did not observe any trend toward MTL activity in our conventional subsequent memory analysis (hits versus misses). The results of this analysis were used as an inclusive mask [48,49,47] in order to identify only those regions where WF and strength effects co-existed with encoding effects. This also served the purpose of substantially reducing the probability of false positives in these analyses by limiting the number of voxels that were searched. However, when the WF analysis was conducted without masking, we did observe an increased BOLD response in the left anterior hippocampal formation for hits to LF versus HF words (MNI coordinates of $-27, -15, -9$; $Z=3.09, p=0.001$), with a focus very similar to that reported by previous studies of verbal encoding, such as Otten et al. [48] (MNI coordinates of $-27, -15, -12$). Conversely, no MTL activity was observed for the strength comparisons with repeated items when masking was omitted.

As no trend toward MTL activity was observed in the subsequent memory analysis that had greater sensitivity to detect an item encoding effect, it appears unlikely that the significant MTL response observed for the WF effect, if it is not a false positive, can be attributed to item encoding associated with the modestly higher hit-rate for LF words in the present study ($\sim 12.5\%$) [61]. An explanation in terms of increased recollection [56] also appears unlikely as recollection has been proposed to contribute to the subsequent memory effect [56,72], and because of the failure to observe MTL responses in the comparison of repeated items at study, as recollection is assumed to be strengthened by item repetition [56,72]. However, recollection is viewed as not contributing to the LF word HR advantage in other models [40].

It should be noted that MTL responses have also been reported during performance of attentional and working memory tasks, suggesting that the representations accessed by the MTL are not necessarily mnemonic ones [6]. Moscovitch [43] proposed that the MTL is instead a module responsible for automatically registering the contents of consciousness. If the MTL activity observed in conjunction with the WF effect reflects indexing of conscious representations, then it is plausible that the unusual features of LF words require relatively greater processing to register than their HF word counterparts. This interpretation is consistent with findings that processing times for LF words are longer than HF words in lexical decision and reading tasks

[3,9,50], and theoretical proposals that LF words have more features marked than HF words during encoding [28,38]. However, this registering of item contents into consciousness is not directly associated with their encoding, a role filled more prominently by the LIPC that directs attention selectively to certain item features [70]. Both remembered and unrecognised items presumably engage the registration process upon presentation (see Ref. [6] for a discussion), hence the failure to observe a significant difference in MTL response in our subsequent memory analysis (hits>misses) and in other studies [57]. Our interpretation therefore represents an alternative view of the relationship between the LIPC and MTL structures to one that considers the LIPC to transfer information to the MTL for “binding” into long-term memory [5].

4.4. Concluding comments

In this paper, we have attempted to test some assumptions of several different memory theories that provide explanations of the WF and strength effects based upon processes that occur hypothetically during encoding [28,37,39,41,62]. Explanations for both effects have traditionally been the domain of single-process theories [15,28,37,42,63], although dual-process accounts have emerged recently [7,34,40,55]. The increased BOLD response in the LIPC associated with the LF word HR advantage supports the AE explanation of the WF effect [28,37,39,41,62].

Medial but not lateral parietal cortex responses were observed for repeated items (here interpreted as an index of encoding strength), indicating it is unlikely that study involves accessing prior representations of repeated items via the same mechanism as that at test [42], or involves a conscious recall-like process such as recollection [40]. Each presentation of an item may instead be stored separately [35,51]. However, less attention or processing effort does appear to be required for encoding each repeated presentation of an item [7], as reduced BOLD responses were observed in the LIPC and lateral middle temporal cortex—regions that demonstrated increased activity during the conventional subsequent memory analysis. Finally, while item repetition tends to be discussed chiefly in relation to the proposed strengthening it has upon a memory trace [7,42,63], the act of repeating an item may itself be encoded [32], along with knowledge of the spacing of repetitions [31], both factors we were unable to address in the present study. Future neuroimaging investigations might explore these important memory effects in detail using established memory paradigms.

Acknowledgments

We are grateful to Brendan Miller, Yvette Stonier, Sonya Faint and Michael Walsh for their assistance with conduct-

ing the study. This study was supported by Australian Research Council (ARC) Discovery Project Grant DP0342656. Greig de Zubicaray is supported by an ARC Research Fellowship.

References

- [1] J.L.R. Andersson, C. Hutton, J. Ashburner, B. Turner, K. Friston, Modeling geometric deformations in EPI time series, *Neuroimage* 13 (2001) 903–919.
- [2] J. Ashburner, K.J. Friston, Nonlinear spatial normalization using basis functions, *Hum. Brain Mapp.* 7 (1999) 254–266.
- [3] D. Besner, R.S. McCann, Word frequency and pattern distortion in visual word identification and production: an examination of four classes of models, in: M. Coltheart (Ed.), *Attention and Performance: XII. The Psychology of Reading*, Earlbaum, Hillsdale, 1987, pp. 201–220.
- [4] M.W. Brown, J.Z. Xiang, Recognition memory: neuronal substrates of the judgement of prior occurrence, *Prog. Neurobiol.* 55 (1998) 149–189.
- [5] R.L. Buckner, W.M. Kelley, S.E. Petersen, Frontal cortex contributes to human memory formation, *Nat. Neurosci.* 2 (1999) 311–314.
- [6] R. Cabeza, F. Dolcos, S.E. Prince, H.J. Rice, D.H. Weissman, L. Nyberg, Attention-related activity during episodic memory retrieval: a cross-function fMRI study, *Neuropsychologia* 41 (2003) 390–399.
- [7] M. Cary, L.M. Reder, A dual-process account of the list-length and strength-based mirror effects in recognition, *J. Mem. Lang.* 49 (2003) 231–248.
- [8] K.A. Chalmers, M.S. Humphreys, Role of generalised and episode specific memories in the word frequency effect in recognition, *J. Exp. Psychol.: Learn Mem. Cogn.* 24 (1998) 610–632.
- [9] M.W.L. Chee, N.H.H. Hon, D. Caplan, H. Ling Lee, J. Goh, Frequency of concrete words modulates prefrontal activation during semantic judgements, *Neuroimage* 16 (2002) 259–268.
- [10] S.E. Clark, R.M. Shiffrin, Cueing effects and associative information in recognition memory, *Mem. Cogn.* 20 (1992) 580–598.
- [11] D.A. Copland, G.I. de Zubicaray, K.L. McMahon, M.M. Eastburn, S.J. Wilson, H.J. Chenery, Brain activity during automatic semantic priming revealed by event-related fMRI, *Neuroimage* 20 (2003) 302–310.
- [12] F.I. Craik, R. Govoni, M. Naveh-Benjamin, N.D. Anderson, The effects of divided attention on encoding and retrieval processes in human memory, *J. Exp. Psychol. Gen.* 125 (1996) 159–180.
- [13] L. Davachi, A.D. Wagner, Hippocampal contributions to episodic encoding: insights from relational and item-based learning, *J. Neurophysiol.* 88 (2002) 982–990.
- [14] S. Dennis, The Sydney Morning Herald Word Database. *Noetica: Open Forum* 1 (1995) <http://psy.uq.edu.au/CogPsych/Noetica>.
- [15] S. Dennis, M.S. Humphreys, A context noise model of episodic word recognition, *Psychol. Rev.* 108 (2001) 452–478.
- [16] J.T. Devlin, P.M. Matthews, M.F. Rushworth, Semantic processing in the left inferior prefrontal cortex: a combined functional magnetic resonance imaging and transcranial magnetic stimulation study, *J. Cogn. Neurosci.* 15 (2003) 71–84.
- [17] I.G. Dobbins, H.J. Rice, A.D. Wagner, D.L. Schacter, Memory orientation and success: separable neurocognitive components underlying episodic recognition, *Neuropsychologia* 41 (2003) 318–333.
- [18] L.L. Eldridge, B.J. Knowlton, C.S. Furmanski, S.Y. Bookheimer, S.A. Engel, Remembering episodes: a selective role for the hippocampus during retrieval, *Nat. Neurosci.* 3 (2000) 1149–1152.
- [19] W.K. Estes, W.T. Maddox, On the processes underlying stimulus—familiarity effects in recognition of words and nonwords, *J. Exp. Psychol.: Learn. Mem. Cogn.* 28 (2002) 1003–1018.
- [20] A.C. Evans, M. Kamber, D.L. Collins, D. Macdonald, An MRI-based probabilistic atlas of neuroanatomy, in: S. Shorvon, D. Fish, F.

- Andermann, G.M. Bydder, H. Stefan (Eds.), *NATO ASI Series A, Life Sciences, Magnetic Resonance Scanning and Epilepsy*, vol. 264, Plenum, New York, 1994, pp. 263–274.
- [21] C.J. Fiebach, A.D. Friederici, K. Muller, D.Y. von Cramon, fMRI evidence for dual routes to the mental lexicon in visual word recognition, *J. Cogn. Neurosci.* 14 (2002) 11–23.
- [22] J.A. Fiez, Phonology, semantics, and the role of the left inferior prefrontal cortex, *Hum. Brain Mapp.* 5 (1997) 79–83.
- [23] J.A. Fiez, D.A. Balota, M.E. Raichle, S.E. Petersen, Effects of lexicality, frequency, and spelling-to-sound consistency on the functional anatomy of reading, *Neuron* 24 (1999) 205–218.
- [24] K.J. Friston, J. Ashburner, C.D. Frith, J.-B. Poline, J.D. Heather, R.S.J. Frackowiak, Spatial registration and normalization of images, *Hum. Brain Mapp.* 2 (1995) 165–189.
- [25] K.J. Friston, P.C. Fletcher, O. Josephs, A. Holmes, M.D. Rugg, R. Turner, Event-related fMRI: characterising differential responses, *Neuroimage* 7 (1998) 30–40.
- [26] K.J. Friston, D.E. Glaser, R.N.A. Henson, S. Kiebel, C. Phillips, J. Ashburner, Classical and Bayesian inference in neuroimaging: applications, *Neuroimage* 16 (2002) 484–512.
- [27] J.D. Gabrieli, R.A. Poldrack, J.E. Desmond, The role of left prefrontal cortex in language and memory, *Proc. Natl. Acad. Sci. U. S. A.* 95 (1998) 906–913.
- [28] M. Glanzer, J.K. Adams, The mirror effect in recognition memory: data and theory, *J. Exp. Psychol.: Learn. Mem. Cogn.* 16 (1990) 5–16.
- [29] R.N. Henson, Neuroimaging studies of priming, *Prog. Neurobiol.* 70 (2003) 53–81.
- [30] R.N. Henson, T. Shallice, R.J. Dolan, Right prefrontal cortex and episodic memory retrieval: a functional MRI test of the monitoring hypothesis, *Brain* 122 (1999) 1367–1381.
- [31] D.L. Hintzman, R.A. Block, Memory for the spacing of repetitions, *J. Exp. Psychol.* 99 (1973) 70–74.
- [32] D.L. Hintzman, T. Curran, When encoding fails: instructions, feedback, and registration without learning, *Mem. Cogn.* 23 (1995) 213–226.
- [33] F. Jessen, S. Flacke, D.O. Granath, C. Manka, L. Scheef, A. Papassotiropoulos, H.H. Schild, R. Heun, Encoding and retrieval related cerebral activation in continuous verbal recognition, *Cogn. Brain Res.* 12 (2001) 199–206.
- [34] S. Joordens, W.E. Hockley, Recollection and familiarity through the looking glass: when old does not mirror new, *J. Exp. Psychol.: Learn. Mem. Cogn.* 26 (2000) 1534–1555.
- [35] T.K. Landauer, Memory without organization: properties of a model with random storage and undirected retrieval, *Cogn. Psychol.* 7 (1975) 495–531.
- [36] M. Lepage, O. Ghaffar, L. Nyberg, E. Tulving, Prefrontal cortex and episodic memory retrieval mode, *Proc. Natl. Acad. Sci. U. S. A.* 97 (2000) 506–511.
- [37] W.T. Maddox, W.K. Estes, Direct and indirect stimulus–frequency effects in recognition, *J. Exp. Psychol.: Learn. Mem. Cogn.* 23 (1997) 539–559.
- [38] K.J. Malmberg, K. Murnane, List composition and the word-frequency effect for recognition memory, *J. Exp. Psychol.: Learn. Mem. Cogn.* 28 (2002) 616–630.
- [39] K.J. Malmberg, T.O. Nelson, The word frequency effect for recognition memory and the elevated-attention hypothesis, *Mem. Cogn.* 31 (2003) 35–43.
- [40] K.J. Malmberg, J.E. Holden, R.M. Shiffrin, Modeling the effects of repetitions, similarity, and normative word frequency on judgments of frequency and recognition memory, *J. Exp. Psychol.: Learn. Mem. Cogn.* 30 (2004) 319–331.
- [41] G. Mandler, Recognizing: the judgment of previous occurrence, *Psychol. Rev.* 87 (1980) 252–271.
- [42] J.L. McClelland, M. Chappell, Familiarity breeds differentiation: a subjective-likelihood approach to the effects of experience in recognition memory, *Psychol. Rev.* 105 (1998) 724–760.
- [43] M. Moscovitch, Memory and working with memory: a component process model based on modules and central systems, *J. Cogn. Neurosci.* 4 (1992) 257–267.
- [44] B. Murdock, M. Lamon, The replacement effect: repeating some items while replacing others, *Mem. Cogn.* 16 (1988) 91–101.
- [45] S. Ogawa, T.M. Lee, A.R. Kay, D.W. Tank, Brain magnetic resonance imaging with contrast dependent on blood oxygenation, *Proc. Natl. Acad. Sci. U. S. A.* 3 (1990) 9868–9872.
- [46] G.A. Ojemann, J. Schoenfield-McNeill, D.P. Corina, Anatomic subdivisions in human temporal cortical neuronal activity related to recent verbal memory, *Nat. Neurosci.* 5 (2002) 64–71.
- [47] L.J. Otten, M.D. Rugg, Task-dependency of the neural correlates of episodic encoding as measured by fMRI, *Cereb. Cortex* 11 (2001) 1150–1160.
- [48] L.J. Otten, R.N. Henson, M.D. Rugg, Depth of processing effects on neural correlates of memory encoding: relationship between findings from across- and within-task comparisons, *Brain* 124 (2001) 399–412.
- [49] L.J. Otten, R.N. Henson, M.D. Rugg, State-related and item-related neural correlates of successful memory encoding, *Nat. Neurosci.* 5 (2002) 1339–1344.
- [50] K.R. Paap, J.E. McDonald, R.W. Schvanveldt, R.W. Noel, Frequency and pronounceability in visually presented naming and lexical decision tasks. Word frequency and pattern distortion in visual word identification, in: M. Coltheart (Ed.), *Attention and Performance: XII. The Psychology of Reading*, Earlbaum, Hillsdale, 1987, pp. 221–244.
- [51] J.G.W. Raaijmakers, Spacing and repetition effects in human memory: application of the SAM model, *Cogn. Sci.* 27 (2003) 431–452.
- [52] C. Ranganath, G. Rainer, Neural mechanisms for detecting and remembering novel events, *Nat. Rev., Neurosci.* 4 (2003) 193–202.
- [53] R. Ratcliff, W. Hockley, G. McKoon, Components of activation: repetition and priming effects in lexical decision and recognition, *J. Exp. Psychol. Gen.* 114 (1985) 435–450.
- [54] P.J. Reber, R.M. Siwieg, D.R. Gitelman, T.B. Parrish, M.M. Mesulam, K.A. Paller, D.R. Gitelman, Neural correlates of successful encoding identified using functional magnetic resonance imaging, *J. Neurosci.* 22 (2002) 9541–9548.
- [55] L.M. Reder, A. Nhuyvanisvong, C.D. Schunn, M.S. Ayers, P. Angstadt, K. Hiraki, A mechanistic account of the mirror effect for word frequency: a computational model of remember-know judgments in a continuous recognition paradigm, *J. Exp. Psychol.: Learn. Mem. Cogn.* 26 (2000) 294–320.
- [56] M.D. Rugg, A.P. Yonelinas, Human recognition memory: a cognitive neuroscience perspective, *Trends Cogn. Sci.* 7 (2003) 313–319.
- [57] M.D. Rugg, L.J. Otten, R.N. Henson, The neural basis of episodic memory: evidence from functional neuroimaging, *Philos. Trans. R. Soc. Lond. Ser. B: Biol. Sci.* 357 (2002) 1097–1110.
- [58] M.D. Rugg, R.N. Henson, W.G. Robb, Neural correlates of retrieval processing in the prefrontal cortex during recognition and exclusion tasks, *Neuropsychologia* 41 (2003) 40–52.
- [59] D.L. Scarborough, C. Cortese, H.S. Scarborough, Frequency and repetition effects in lexical memory, *J. Exp. Psychol. Hum. Percept. Perform.* 3 (1977) 1–17.
- [60] D.L. Schacter, R.D. Badgaiyan, Neuroimaging of priming: new perspectives on implicit and explicit memory, *Curr. Dir. Psychol. Sci.* 10 (2001) 1–4.
- [61] D.L. Schacter, A.D. Wagner, Medial temporal lobe activations in fMRI and PET studies of episodic encoding and retrieval, *Hippocampus* 9 (1999) 7–24.
- [62] R.N. Shepard, Recognition memory for words, sentences, and pictures, *J. Verbal Learn. Verbal Behav.* 6 (1967) 156–163.
- [63] R.M. Shiffrin, M. Steyvers, A model for recognition memory: REM: retrieving effectively from memory, *Psychon. Bull. Rev.* 4 (1997) 145–166.
- [64] B.A. Strange, L.J. Otten, O. Josephs, M.D. Rugg, R.J. Dolan, Dissociable human perirhinal, hippocampal, and parahippocampal roles during verbal encoding, *J. Neurosci.* 22 (2002) 523–528.

- [65] V. Stretch, J.T. Wixted, On the difference between strength-based and frequency-based mirror effects in recognition memory, *J. Exp. Psychol.: Learn Mem. Cogn.* 24 (1998) 1379–1396.
- [66] P. Thévanaz, T. Blu, M. Unser, Interpolation revisited, *IEEE Trans. Med. Imag.* 19 (2000) 739–758.
- [67] S.L. Thompson-Schill, M. D'Esposito, I.P. Kan, Effects of repetition and competition on activity in left prefrontal cortex during word generation, *Neuron* 23 (1999) 513–522.
- [68] D.C. Van Essen, H.A. Drury, J. Dickson, J. Harwell, D. Hanlon, C.H. Anderson, An integrated software suite for surface-based analyses of cerebral cortex, *J. Am. Med. Inform. Assoc.* 8 (2001) 443–459.
- [69] A.D. Wagner, W. Koutstaal, D.L. Schacter, When encoding yields remembering: insights from event-related neuroimaging, *Philos. Trans. R. Soc. Lond. Ser. B: Biol. Sci.* 354 (1999) 1307–1324.
- [70] A.D. Wagner, A. Maril, D.L. Schacter, Interactions between forms of memory: when priming hinders new episodic learning, *J. Cogn. Neurosci.* 12 (Suppl. 2) (2000) 52–60.
- [71] M.E. Wheeler, R.L. Buckner, Functional dissociation among components of remembering: control, perceived oldness, and content, *J. Neurosci.* 23 (2003) 3869–3880.
- [72] A.P. Yonelinas, The nature of recollection and familiarity: a review of 30 years of research, *J. Mem. Lang.* 46 (2002) 441–517.