Research Report

fMRI evidence of word frequency and strength effects in recognition memory

Greig I. de Zubicaray*, Katie L. McMahon, Matthew M. Eastburn, Simon Finnigan, Michael S. Humphreys

*Centre for Magnetic Resonance, The University of Queensland, QLD, 4072, Australia
bCentre for Human Factors and Applied Cognitive Psychology, The University of Queensland, QLD, Australia

Abstract

We used event-related fMRI to investigate the neural correlates of encoding strength and word frequency effects in recognition memory. At test, participants made Old/New decisions to intermixed low (LF) and high frequency (HF) words that had been presented once or twice at study and to new, unstudied words. The Old/New effect for all hits vs. correctly rejected unstudied words was associated with differential activity in multiple cortical regions, including the anterior medial temporal lobe (MTL), hippocampus, left lateral parietal cortex and anterior left inferior prefrontal cortex (LIPC). Items repeated at study had superior hit rates (HR) compared to items presented once and were associated with reduced activity in the right anterior MTL. By contrast, other regions that had shown conventional Old/New effects did not demonstrate modulation according to memory strength. A mirror effect for word frequency was demonstrated, with the LF word HR advantage associated with increased activity in the left lateral temporal cortex. However, none of the regions that had demonstrated Old/New item retrieval effects showed modulation according to word frequency. These findings are interpreted as supporting single-process memory models proposing a unitary strength-like memory signal and models attributing the LF word HR advantage to the greater lexico-semantic context-noise associated with HF words due to their being experienced in many pre-experimental contexts.

1. Introduction

Recognition memory experiments typically involve participants studying a list of words and, following a delay, being tested with a series of words that were included in the study list and some that were not. The participants decide which of these words they have seen before and which are unstudied words. These experiments have revealed two important phenomena: Repeating words presented in a study list increases their hit rate (HR; correct responses to studied words) at test, and HRs are superior for low frequency (LF) than high frequency (HF) words. In addition, unstudied LF words are less likely than unstudied HF words to be judged incorrectly as belonging to the study list (a “false alarm”; FA)—an example of a mirror effect [22]. When between-list experimental designs are employed, a mirror effect is also observed for repeated items [5,58]. Many memory theories hypothesise that item repetition strengthens episodic memory representations by either adding features to an existing trace or storing a novel one [34,47,54]). The single-process models proposed by Shiffrin and Steyvers (“retrieving effectively from memory” or REM) [54] and McClelland and Chappell [43] are examples of this approach. Single-process models of memory assume the existence of a unitary, continuous multi-component model of memory.

Theme: Neural basis of behaviour
Topic: Cognition
Keywords: Word frequency; Recognition; Episodic memory; Encoding strength; fMRI; Recollection; Familiarity

* Corresponding author. Fax: (+617) 3365 3833.
E-mail address: greig.dezubicaray@cmr.uq.edu.au (G.I. de Zubicaray)
memory trace or signal. Conversely, dual-process theories consider episodic memory strength to involve contributions from putatively separate strength-like (familiarity) and recall-like (recollection) processes [5,29,31,49,67]. For example, in Malmberg et al.’s [41] dual-process extension of the REM model, recollection serves the purpose of assessing the content of an episodic trace. As content becomes stronger with increasing storage of item features (familiarity), a better assessment of the features can be provided (recollection), assisting correct rejection of unstudied items at test. Item repetition is also considered to strengthen both familiarity and recollection in the dual-process models proposed by Reder et al. (“source of activation confusion” or SAC [5,49]) and Yonelinas [67], with recollection accounting for a relatively greater proportion of hits to repeated words than familiarity.

Accounts of the LF word hit rate advantage vary between theories. Some propose it to be a result of relatively greater attentional allocation to the features of LF words at encoding (e.g., Attention Likelihood Theory or ALT [22]; see also [16,39,40]), while others attribute it to processes occurring solely at test (e.g., “bind-cue-decide in memory” or BCDMEM [9]) or a combination of both [5,41]. For example, the original single-process REM model attributed the effect to familiarity due to the relatively more diagnostic or distinctive features of LF words [54]. In the dual-process extension of REM, this explanation is maintained: the recall or recollection mechanism does not favour LF words [41]. However, this view contrasts with several other dual-process models that consider LF words to be more recollectable than HF words [5,31].

An alternative class of memory model – the context noise model – makes different assumptions about the mechanisms responsible for word frequency and repetition effects in recognition memory [9]. Both item and context information are incorporated in a number of memory models [5,41], although most emphasise the role of the former type of information, and are hereafter referred to as item-noise models. Item information pertains to the features (e.g., orthographic, graphemic) describing each word, whereas context information might be best considered a lexical-semantic construct referring to the manner in which a word is used, related to word frequency [57]. For example, the word spanner is used in a relatively specialised way in conversations or text concerning tool use or engineering, whereas the word morning is likely to be used in many different scenarios. Item-noise models assume the majority of interference or noise in memory is caused by other items presented in the study list, whereas context-noise models (e.g., BCDMEM [9]) assume this sort of interference is negligible (see also Sikström [55]). To explain the LF word hit rate advantage, BCDMEM assumes that HF words are subject to greater interference due to the number of pre-experimental contexts in which they have been encountered [9]. In this account, a cue consisting of context information is used to search memory in order to retrieve an episodic trace at test, the traces similar to the information in the cue become activated, and this information contributes to the recognition decision. As LF words tend to have been encountered in fewer pre-experimental contexts, they are more strongly associated with the study context and the context that the participant reinstates at test. Thus, their traces receive relatively greater activation compared to those of HF words. However, strengthening the association between a word and the experimental context by repeating it at study is not considered to interfere with the memory retrieved to a different word in the list [9].

Information about the neurophysiological mechanisms contributing to recognition memory is being used increasingly to constrain and support theoretical perspectives [45,52]. Functional magnetic resonance imaging (fMRI) experiments have contrasted cerebral activity associated with studied and unstudied items, revealing consistent involvement of discrete anterior, superior and inferior regions of the prefrontal cortex, the left lateral and medial (cuneus/precuneus) parietal cortex and, less consistently, the medial temporal lobe (MTL) [11,15,25]. The respective roles of the prefrontal regions have been the subject of debate concerned with differentiating initial-retrieval- from post-retrieval-related processes. For example, the right superior region might be involved in monitoring and evaluating the products of a retrieval attempt [52], while activity in the left inferior prefrontal cortex (LIPC) might represent retrieval success or the outcome of the retrieval attempt [12,52]. A more tonic “episodic retrieval mode”, a mental set or state deemed necessary for remembering studied items, is proposed to be mediated by a right anterior region (frontal polar cortex) [38]. Cortical correlates of the dual-process theoretical constructs of recollection and familiarity have also been proposed based upon results from these experiments. Responses in the left lateral inferior parietal cortex and, less frequently, in the hippocampal formation in the MTL (when observed) have been attributed to recollection, while activity in adjacent MTL structures such as the amygdala, rhinal and parahippocampal cortices is proposed to represent a familiarity-based signal [15,26,45,52]. A potential dissociation of these responses in terms of their direction has also been proposed: whereas recollection is reflected in positive activity for studied vs. unstudied items, the familiarity response shows the opposite relationship [26,52]. This is viewed as being consistent with the assumption that familiarity and implicit priming represent similar memory processes [42], as implicit priming effects are usually associated with reductions in cerebral activity in fMRI experiments [24,48]. Although Rugg and Yonelinas [52] have explicitly attributed retrieval-related activity in the left parietal cortex to recollection, it is worth noting that contradictory evidence exists. For example, several recent studies have failed to observe retrieval success effects in this region (e.g., [11,32,64,65]), and Wheeler and Buckner [64] recently proposed an alternative interpretation based upon the
observation that this region demonstrated activity associated with all Old responses at test, that is, irrespective of whether items were studied or unstudied. They suggested that activity in the left parietal cortex instead modulates on the basis of the perception of oldness. Finally, while the LIPC has not been linked explicitly with either recollection or familiarity by memory theorists [45,52], its putative role in controlled retrieval of both semantic and non-semantic information in episodic memory may indicate a relation to these processes [62,64,65]. Some dual-process theories assume recollection reflects a consciously controlled process, while familiarity is relatively automatic [29,67].

Lesion studies have indicated a prominent role for the left lateral temporal cortex (LTC) in the representation of semantic knowledge [36,53]. Similarly, cognitive neuroscience experiments have implicated this region in lexical-semantic processing consistently across a variety of tasks, including lexical decision (word vs. nonword; [50]), semantic priming (related vs. unrelated words; [7]), spoken word production [35] and episodic memory retrieval [44]. If recognition memory is cued with context information, resulting in episodic traces with lexical-semantic information similar to the cue being activated, then this region seems a plausible candidate for mediating the LF word HR advantage assuming there is greater lexico-semantic context noise associated with HF compared to LF words [9]. Given the LIPC has been reported to be active during tasks requiring controlled retrieval of semantic and other information, it might also be considered a potential candidate for mediating context-cued retrieval. However, it is not clear how such a role might be differentiated from another putative role in recollection (see above).

The present experiment represents a companion to a previous event-related fMRI investigation in which we reported word frequency and strength effects at episodic encoding [10]. In that paper, we tested predictions from single- and dual-process models that attributed these effects in recognition memory to processes occurring during study. For example, Glanzer et al.’s [22] ALT theory proposes that the LF word HR advantage is due to relatively greater attention directed selectively to the features of LF words at encoding (see also [16,39,40]), while Cary and Reder’s dual-process model [5] assumes that less processing effort is entailed for encoding each repetition of an item. Both of these assumptions were supported by the fMRI data [10]. Here, we use retrieval phase data acquired during the same experiment to test several predictions derived from single- and dual-process models that attribute strength and word frequency effects in recognition memory explicitly to processes occurring at test. Relatively few fMRI studies have examined encoding and retrieval effects in the same participants [6]. According to several dual-process theories, repetition strengthens both familiarity and recollection processes at test [5,41,67]. Given the evidence from the cognitive neuroscience investigations reviewed above, this should be reflected in differential activity in the anterior MTL and hippocampal formation at test for items presented either once or twice at study, and perhaps also in the lateral parietal cortex and anterior LIPC. Specifically, the latter three regions should show increases in activity associated with greater recollection for repeated words, whereas the anterior MTL should show a reduction in activity with increasing familiarity [26,52]. Single-process models assume item repetition to strengthen a unitary, continuous multi-component memory trace analogous to familiarity [43,54]. With respect to the LF word HR advantage, dual-process theories provide conflicting predictions: according to the dual-process extension of the REM model [41], the effect is due solely to greater familiarity for the relatively more diagnostic features of LF words. This should therefore be reflected in reduced activity in the anterior MTL. Other dual-process models consider LF words to be more recollectable [31,49], which should be reflected in increased activity in the hippocampal formation and perhaps also lateral parietal cortex [52] and anterior LIPC. By contrast, the BCDMEM model does not predict differences in item-level effects for LF versus HF words, instead attributing the LF word HR advantage to differential effects of lexico-semantic context-dependent processing [9]. Thus, the greater noise associated with HF words due to their being experienced in multiple prior contexts should be reflected in reduced activity in the left LTC compared to LF words.

2. Materials and methods

2.1. Participants

Fourteen right-handed volunteers (7 female) from the University of Queensland community participated. Volunteers ranged in age from 21 to 38 years (mean age 28.6 years) were native English speakers, with no history of neurological or psychiatric disorders. They provided informed consent in accordance with procedures approved by the University of Queensland’s Medical Research Ethics Committee and were reimbursed AUD $30 for their participation.

2.2. Task and procedure

Prior to scanning, participants performed a brief practice session involving studying 3 words each of single and repeated presentation LF and HF words, followed by a test list comprising these words and 3 new HF and LF words. During scanning, participants performed three consecutive study/test sessions, with a brief rest break (1 to 2 min) between sessions. The experiment procedures were identical to those described in de Zubicaray et al. [10]. A total of 72 words were presented during each study phase, of which 48 were unique words (24 per frequency condition) with 12 LF and 12 HF words presented once, and 12 LF and 12 HF words presented twice. All words were presented for 800 ms with an ISI of 2200 ms during which participants viewed a
Each acquisition were discarded in order to allow magneti
dependent contrast (T2*). The first five volumes from
time, 40 ms; flip angle, 90°
imaging (EPI) sequence (repetition time, 2100 ms; echo
(0.5 mm gap) were acquired using a gradient echo planar
sessions, 300 whole-brain volumes (64 x 64 matrix; 3.75 x
2.4. Image acquisition

2.3. Apparatus

Word stimuli were presented and responses from an MR-compatible dual button box were recorded using a laptop PC running Microsoft Visual Basic and ExacTicks (Ryle Design) software. Stimuli were presented in black font on a white background and projected using a BenQ SL705X projector onto a screen at the foot of the magnet bore that participants viewed through a mirror mounted on the head coil, subtending approximately 10° of visual arc.

2.4. Image acquisition

Functional imaging was conducted on a 1.5-T Siemens Sonata system (Erlangen, Germany). In three consecutive sessions, 300 whole-brain volumes (64 x 64 matrix; 3.75 x 3.75 mm voxels) consisting of 21 near axial 5 mm slices (0.5 mm gap) were acquired using a gradient echo planar imaging (EPI) sequence (repetition time, 2100 ms; echo time, 40 ms; flip angle, 90°) sensitive to blood oxygen level dependent contrast (T2*). The first five volumes from each acquisition were discarded in order to allow magneti-
sation to stabilise. Head movement was limited by foam
inserts within the head coil. Structural images were next acquired using a magnetisation prepared rapid acquisition gradient echo (MP-RAGE) T1-weighted sequence (256 x
matrix; 0.9 mm3 voxels).

2.5. fMRI data analysis

Data were pre-processed and analysed using statistical
parametric mapping software (SPM2, Wellcome Depart-
ment of Cognitive Neurology, Queens Square, London, UK). Time-series images from the three sessions were slice-
timing corrected [59], then realigned and variance attribut-
able to movement-by-susceptibility interactions removed
(“realign and unwarp” option; [1,19]). A mean image was
generated from these data, and spatially normalised to the
SPM2 EPI template image in MNI atlas space [2,17]. The
non-linear transformations were next applied to the time-
series images from which the mean had been generated.
Images were resampled to 3 mm3 voxels and spatially
smoothed with an 8 mm full width half maximum (FWHM)
isotropic Gaussian kernel.

Statistical analyses were performed using the general
linear model [21]. The hits (correct “old” responses to
studied words), misses (incorrect “new” responses to studied words), false alarms (FA; incorrect “old” responses to
unstudied words) and correct rejections (CR; “new” responses to unstudied words) from each test condition and
presentation (single and repeated presentation and new LF
and HF words) were modelled using a synthetic hemody-
namic response function (HRF) and its temporal and
dispersion derivatives [20]. The trials from each study
condition and presentation were also modelled in a similar
manner and the results are reported elsewhere [10]. Effects
were estimated using subject-specific fixed-effects models
with standard high- and low-pass filtering applied. Linear
contrasts of the parameter estimates of the HRF from each
subject were used in second-stage group-level random effects
analyses. These consisted of one-sample t tests, and the
t values were transformed into corresponding Z scores.
Effects exceeding a one-tailed alpha threshold of 0.001
(Z > 3.09, uncorrected for multiple comparisons) and con-
sisting of >8 contiguous voxels were considered reliable.

The Old/New effect was determined by comparing all hits
to CRs (i.e., collapsed across word frequency and repetition
conditions). Regions-of-interest (ROIs) corresponding to
areas that, a priori, were expected to demonstrate item
retrieval effects in the strength and word frequency (WF)
alyses were derived from this group-level contrast in order
to ensure that any effects co-existed with Old/New effects.
These ROIs (lateral parietal cortex, anterior MTL, hippo-
campl formation, anterior LIPC) were generated using an
alpha threshold of 0.005 (Z > 2.58, uncorrected) in order to
permit potential responses in the MTL to be included, given
the lower SNR observed in this region compared to adjacent
cortical structures [11]. Each ROI was defined using a sphere
with a radius of 6 mm from the respective peak activation value. For each subject, the mean signal in the ROI was calculated for the relevant experimental conditions using Marsbar software (http://www.marsbar.sourceforge.net; [3]), and subjected to paired \( t \) tests. To identify strength-related effects, hits to single vs. repeated presentation words were compared, irrespective of frequency. For the WF effect, hits to LF words were compared to hits to HF words, collapsed across repetitions. In addition to the ROI analyses listed above, whole-brain exploratory analyses of item retrieval effects were conducted by inclusively masking the results of the WF and strength analyses with the results of the Old/New comparison (thresholded at \( P < 0.005 \), for the above-mentioned reasons). In order to identify context rather than item retrieval effects in the WF comparison, the result of the WF analysis was exclusively masked with the outcome of the Old/New items analysis (thresholded at \( P < 0.05 \)). This lower significance level increases the confidence with which it can be concluded that the two contrasts do not overlap. We do not report comparisons of New, unstudied items, as single- and dual-process models both assume CRs reflect the absence of memory traces associated with the study list [30,54]. The results of the whole-brain analyses were rendered onto surface-based representations generated using computerised anatomical reconstruction and editing toolkit software (CARET; [61]).

3. Results

3.1. Behavioural data

Table 1 shows the HR results of this experiment. Collapsed across word frequency and strength conditions, the overall HR was 0.817. As expected, a mirror-patterned WF effect was observed overall. An ANOVA on HRs showed main effects of word frequency, \( F(1, 13) = 4.34 \),

<table>
<thead>
<tr>
<th>Word frequency</th>
<th>Weak</th>
<th>Strong</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>High frequency hits</td>
<td>0.687</td>
<td>0.855</td>
<td>0.771</td>
</tr>
<tr>
<td>Low frequency hits</td>
<td>0.812</td>
<td>0.915</td>
<td>0.864</td>
</tr>
<tr>
<td>Mean</td>
<td>0.749</td>
<td>0.885</td>
<td>0.817</td>
</tr>
</tbody>
</table>

Table 1
Recognition hit rates for word frequency and weak and strong conditions

Fig. 1. (A–B) Inflated surface representations of left and right hemisphere cerebral regions demonstrating significant Old > New effects. (C–D) Inflated surface representations of left and right hemisphere cerebral regions demonstrating significant New > Old effects. (E–H) From left to right, coronal slices showing New > Old effects in left parahippocampal gyrus, right parahippocampal gyrus, right amygdala and right hippocampus (refer to text for coordinates and Z scores).
MSE = 0.119, $P < 0.05$, and strength, $F(1, 13) = 9.41$, MSE = 0.259, $P < 0.005$. The interaction between frequency and strength was not significant, $F(1, 13) = 0.546$, MSE = 0.015, $P > 0.05$. 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, $P < 0.001$).

3.2. fMRI data

3.2.1. Old/new effects

The first analysis of the fMRI data examined BOLD responses that differed between studied words that were correctly recognised as old (i.e., hits, collapsed across frequency and strength conditions) and unstudied words that were correctly recognised as new (i.e., CRs) (Fig. 1). This contrast of Hits > CRs revealed activation in posterior cerebral regions including left inferior parietal ($-33, -60, 45; Z = 4.92; BA 7/40$) and bilateral occipital ($-30, -96, 12; Z = 3.68; BA 18$; and $33, -90, 6; Z = 3.76; BA 18/19$) cortices. Multiple anterior left hemisphere regions additionally showed activity including mid-frontal gyrus ($-48, 18, 36; Z = 3.63; BA 9$; and $-30, 51, 3; Z = 3.48; BA 10$), anterior inferior frontal gyrus ($-48, 45, -3; Z = 3.72; BA 10/46$) close to the region reported by Velanova et al. [62] to
be involved in controlled retrieval (coordinates of $-45, 35, -4$; see their Table 1, p. 8463), gyrus rectus ($-12, 45, -15; Z = 3.69; BA 11$), supplementary motor area ($-3, 9, 57; Z = 4.58; BA 8$) and precentral gyrus ($-42, -3, 54; Z = 4.42; BA 6$; and $-51, 3, 27; Z = 3.39$). Other activated regions included the right insula ($33, 21, 3$; $Z = 4.24$) and left caudate ($-18, 33, 0; Z = 4.03$). However, at the lower alpha threshold of 0.005, no evidence of MTL activity was observed for this contrast. In order to determine whether a trend toward an Old/New effect existed, we adopted a much more lenient threshold of 0.01 (uncorrected) following the practice of previous studies \cite{11}. There was no evidence of such a trend using this very lenient threshold.

For the reverse contrast (CRs > Hits), posterior cerebral regions showing activity included the right cuneus ($6, -63, 60; Z = 5.07; BA 7$; and $21, -63, 21; Z = 3.74; BA 31$), left calcarine sulcus ($-18, -66, 18; Z = 4.33; BA 19$), right postcentral gyrus ($27, -45, 54; Z = 3.45$), bilateral supramarginal gyr (54, $-30, 27; Z = 4.79; BA 38$; and $-66, -27, 30; Z = 3.91; BA 40$), right lingual ($24, -54, 0; Z = 4.29; 19/37$) and fusiform gyr (39, $-9, -36; Z = 3.91; BA 21$). Other activated regions included the left precentral gyrus ($-51, -15, 12; Z = 4.27; BA 13$), right mid-temporal gyrus ($48, -69, 21; Z = 4.74; BA 39$; and $51, 6, -30; Z = 3.69$) and bilateral mid-cingulum ($15, -30, 42; Z = 3.74; BA 31$; and $-3, -6, 45; Z = 3.40$). At the lower alpha threshold of 0.005, bilateral anterior MTL foci were observed in the parahippocampal gyrus ($15, 0, -21; Z = 3.66; BA 28$; and $24, -3, -27; Z = 2.83$), amygdala ($30, 3, -21; Z = 3.71; BA$) and hippocampal formation ($24, -15, -18; Z = 3.07$). The right parahippocampal peak maxima was located very near to the coordinates reported by Henson et al. \cite{26} for a familiarity signal in their meta-analysis of four separate experiments ($22, -6, -28$; see their Fig. 1).

3.2.2. LF word HR advantage

In order to examine the effect of the LF word HR advantage (hits to LF vs. HF words, collapsed across repetitions), ROI analyses were conducted upon responses in a priori predicted left lateral parietal cortex, anterior LIPC, anterior MTL, and hippocampal areas demonstrated previously to show Old/New effects (see Methods).\cite{1} None of these regions that had shown item-retrieval effects showed reliable modulation according to frequency: left lateral parietal cortex $t(13) = -1.03, SEM = 0.032, P > 0.05$; anterior LIPC $t(13) = 0.01, SEM = 0.035, P > 0.05$; left parahippocampal gyrus $t(13) = -0.75, SEM = 0.086, P > 0.05$; right parahippocampal gyrus $t(13) = -0.97, SEM = 0.041, P > 0.05$; right amygdala $t(13) = -0.10, SEM = 0.049, P > 0.05$, and right hippocampus $t(13) = -0.56, SEM = 0.062, P > 0.05$ (Fig. 2). The whole-brain analysis of item-retrieval effects (inclusive masked with the outcome of the Old/New items analysis) likewise failed to reveal any significant activation for hits to LF > HF words or the reverse comparison (and at $P < 0.005$). However, when context-retrieval effects were investigated with a whole-brain analysis (exclusively masked with the outcome of the Old/New items analysis), activation was observed in left hemisphere occipital ($-24, -87, 12; Z = 3.90$; and $-18, -99, 21; Z = 3.40$), fusiform ($-39, -60, -18; Z = 3.75$) and middle temporal ($-60, -9, -9; Z = 3.86$; BA 21) gyri (Figs. 3a and b). No significant activation was observed for the reverse comparison (hits to HF > LF words).

3.2.3. Strength effect

The effect of item repetition upon memory strength was likewise investigated in the a priori predicted regions showing Old/New effects using ROI analyses (see Materials and methods). While the right anterior parahippocampal

\footnote{Despite the absence of a significant interaction between word frequency and item strength in the behavioural data, we conducted similar ANOVAs on the fMRI data from the ROIs. None of the ROIs demonstrated significant interactions between frequency and strength (all $F's < 1.8$). Given the absence of significant interactions in either the behavioural or fMRI data, the ROI data were pooled across conditions for the remaining analyses.}
gyrus showed significant modulation according to strength $t(13) = 2.17$, SEM = 0.035, $P < 0.05$, with hits to repeated words demonstrating reduced activation relative to hits to items presented once, none of the other structures examined showed an effect: left lateral parietal cortex $t(13) = 0.40$, SEM = 0.038, $P > 0.05$; left parahippocampal gyrus $t(13) = -0.99$, SEM = 0.098, $P > 0.05$; right amygdala $t(13) = 1.21$, SEM = 0.105, $P > 0.05$, and right hippocampus $t(13) = 1.52$, SEM = 0.049, $P > 0.05$ (Fig. 2). The whole-brain analysis ( inclusively masked with the outcome of the Old/New analysis) also failed to reveal any significant activation in either direction.

4. Discussion

The primary findings in this experiment were that words repeated at study were associated with reduced activity at test in an anterior MTL region compared to words presented once, and that the LF word HR advantage in recognition memory was associated with increased activation in the left lateral temporal cortex. Moreover, other cerebral regions that had evinced reliable Old/New effects did not demonstrate modulation of their activity according to either word frequency or memory strength. These latter regions included the anterior LIPC, left lateral parietal cortex and hippocampal formation—all regions linked by various researchers with the putative process of recollection or controlled retrieval in dual-process models of recognition memory [45,52,62].

4.1. Recognition memory strength

As expected, in the present experiment, repeated items had superior HRs compared to items presented once. Most models of memory assume that repeating items at study strengthens memory traces by either adding features to an existing trace or storing a novel one [34,47,54]. This is the case with single- and dual-process models, although the latter assume that both familiarity (a strength-like process) and recollection (a recall-like process) are strengthened. An anterior MTL response has been associated reliably with correct Old responses to studied items in recognition memory tasks, and is thought to represent a single, strength-like memory factor such as familiarity [26,45,52]. This strength-like response typically manifests as a reduction in cerebral activity for studied compared to unstudied items [26,52], which is viewed by some memory theorists as being consistent with the assumption that familiarity and implicit priming represent similar memory processes [42,52]. Implicit priming effects are generally associated with reductions in cerebral activity [24,48]. The anterior MTL Old/New response that we observed in the right parahippocampal gyrus (peak MNI coordinates of 24, $-3$, $-27$) was located very near to that reported by Henson et al. [26] (see also [52]) for a common familiarity signal in their meta-analysis of the results of four separate recognition memory experiments (peak MNI coordinates of $22$, $-6$, $-28$; see their Fig. 1). This region showed the expected pattern of response, with reduced activation for hits compared to CRs. Importantly, this region also showed significant modulation according to whether items were repeated at encoding, with repeated items showing reduced activity compared to items presented once, that is, a strength effect.

Increased left lateral parietal activity and, less frequently, hippocampal activity associated with correct Old responses is thought to represent the engagement of recollection by dual-process theorists [15,45,52]. Increased activity in the anterior LIPC is likewise thought to represent controlled retrieval, related to recollection [62]. We observed activity in all of these regions in our comparison of hits vs. CRs, consistent with the results of many previous fMRI investigations [11,26,62,64,65]. However, these regions did not demonstrate modulation according to the manipulation of memory strength. In addition, while we did observe a hippocampal response for the Old/New effect, this was opposite in direction (i.e., a decrease) to that reported by Eldridge et al. [15] as representing the process of recollection in their fMRI study that employed a remember-know (RK) paradigm [60]. Donaldson [12] originally suggested that remember (R) and know (K) responses instead represent different levels of decision confidence, or the application of more or less stringent decision criteria in relation to the strength of a single memory trace, and this has been confirmed empirically by Dunn [13,14]. Thus, the results of $R > K$ comparisons in fMRI studies cannot necessarily be interpreted as providing evidence for the operation of two distinct memory processes, as Wixted and Stretch [66] have likewise acknowledged recently in relation to Eldridge et al.’s [15] result (see Discussion). In addition, hippocampal responses have been reported during performance of attentional and working memory tasks in fMRI studies, indicating that the representations accessed by the hippocampus are not invariably mnemonic ones [4,10]. The patterns of activity reported by fMRI studies employing RK paradigms may simply reflect the nature of the question posed to the memory system [28]. Moreover, if recognition memory could be decomposed into two distinct processes, it does not necessarily follow that R and K judgements necessarily index these processes [13,27]. It is worth reiterating that the hippocampus did not show modulation according to item repetition effects in the present experiment, suggesting its activity was unrelated to memory trace strength per se. In fact, hippocampal responses are reported only rarely in association with Old/New item effects in recognition memory, so the implications of this result are presently unclear. Some researchers have suggested that this inconsistency might be due to incidental encoding occurring during recognition impacting upon retrieval-related processes [56].
Collectively, the results of the item strength manipulation provide support for a single strength-like memory factor in recognition and may be interpreted as being inconsistent with the involvement of a separate recall-like process such as recollection (cf. [5,29,31,41,67]). Despite the evidence favouring a single process account, an explanation of item recognition memory effects in terms of familiarity and recollection might still be viable. Wixted and Stretch [66] recently proposed a novel dual-process explanation in which both recollection and familiarity are viewed as continuous processes contributing in combination, rather than separately, to recognition decisions. Nevertheless, like Dunn [14], our preference is for the simpler account when both simple and complex models are equally consistent with the available data.

As we mentioned in Introduction, there may yet be other explanations of memory-related activity in the cerebral regions examined in the present study. Wheeler and Buckner [64,65] recently proposed an alternative interpretation of lateral parietal and anterior LIPC activity in item recognition memory studies. Based upon the observation that these regions demonstrated activity associated with all Old responses at test, that is, irrespective of whether items were studied or unstudied, they suggested that these structures modulate on the basis of the perception of oldness rather than on retrieval success per se, or by extrapolation, recollection (cf. [52]). This interpretation appears consistent with our results, in that both of these regions demonstrated similar levels of retrieval-related activity despite the manipulation of item strength.

4.2. Lexico-semantic context-dependent processing

A significant effect of word frequency upon recognition memory performance was observed in the present experiment. Hit rates were superior for LF than HF words, and unstudied LF words were less likely to produce FAs than unstudied HF words. In short, the well-established mirror effect was observed [22]. However, none of the cerebral regions that demonstrated Old/New effects and were hypothesised to mediate item information retrieval processes demonstrated significant modulation according to word frequency. Hence, the results are at odds with the predictions of single- and dual-process models that attribute the LF word HR advantage to item retrieval processes occurring at test [31,41,43,49,54]. This conclusion applies equally to competing dual-process models that attribute the effect to either familiarity or recollection [31,41,49].

Although no item information retrieval effects were noted, we did observe modulation of several brain regions’ retrieval-related activity according to word frequency. As our primary concern here is with a context-noise explanation, we will confine our discussion of the analyses of the test data to the left lateral temporal cortex, as this region has been implicated repeatedly in lexico-semantic processing and is the most relevant to our hypothesis concerning the LF word HR advantage. As noted in Introduction, lesion and imaging studies have indicated a prominent role for the left lateral temporal cortex in the representation of lexico-semantic knowledge across a range of paradigms [7,36,50,53]. Contrary to single-process item-noise or dual-process models of recognition memory, memory models that assume the LF word HR advantage is due to lexico-semantic context-dependent processing consider HF words to be subject to greater interference at retrieval caused by their being experienced (or encoded) in many different pre-experimental contexts [9,55]. Hence, retrieved LF words are considered to benefit from a stronger association with the study context and the context that the participant reinstates at test. We consider our observation of increased activation in left lateral temporal cortex to be consistent with this account. This result might also be interpreted as providing partial support for the similar assumption made by some dual-process accounts that LF items are easier to recollect because of their being associated with fewer pre-experimental contexts [31,49]. However, as stated previously, none of the regions associated with recollection (anterior LIPC, lateral parietal cortex, hippocampus) showed activity modulated according to frequency.

4.3. Caveats

The present experiment failed to find either strength or word frequency effects in several cerebral areas associated with Old/New effects, including regions deemed to mediate the putative process of recollection. While these are null results, they were obtained using quite sensitive ROI analyses. Although our findings seem reliable, in that some regions showed modulation while others did not, they will need replication to determine their generality. Chee et al. [6] consistently found a null effect of word frequency in regions associated with successful item retrieval (i.e., HRs) across three separate fMRI experiments that used incidental encoding at study (living/non-living judgements). Similarly, they observed no modulation of activity in any of these regions for words that were presented 10 times at study compared to words presented once (see the results of their Experiment 3). However, they did not report anterior MTL activity associated with the Old/New effect, unlike the findings of this and a number of previous experiments [26,52,63]. Although it is still possible that item retrieval processes contribute to the word frequency effect, the available evidence is consistent with the data presented.

2 Although Chee et al. [6] failed to find any activity associated with the LF word HR advantage, they did report differences in activity between LF and HF CRs (i.e., correct New responses to unstudied words) that they suggested might be attributed to the processes of familiarity and recollection. However, according to dual-process theorists, a New response represents the absence of both familiarity and recollection [28]. Single-process theorists similarly assume CRs reflect the absence of episodic memory traces associated with the study list [54].
interpretations of this inconsistency vary, as we also noted retrieval effects and hippocampal activity is mixed, and ing cerebral areas associated with recollection and familiar-
example, by increasing study time.
retrieval (as reviewed by Rugg and Yonelinas [51]), as the studies such as that of Weis et al. [63] have tended to retrieval (correct > incorrect source judgements). Other processes occurring at study and test might contribute to effects in recognition memory, and this information should be considered when developing memory models in the future.

5. Conclusions
In conclusion, the findings of the present experiment indicate that activity in an anterior MTL region is modulated by item memory strength, while a lateral temporal cortex region is associated with the LF word HR advantage in item recognition memory. By contrast, cerebral regions involved reliably in Old/New effects and hypothesised to mediate a putative process of recollection were not modulated by either strength or word frequency. We interpret these results as being consistent with single-process memory models that assume the existence of a unitary, continuous multi-component memory trace or signal, and with models that attribute the LF word HR advantage to the number of pre-experimental lexico-semantic contexts in which words are encountered [9,55]. Whether single-process explanations of other fMRI data considered to support dual-process accounts of recognition memory effects are viable remains to be demonstrated, and should be the subject of future research.
Acknowledgments

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

[34] T.K. Landauer, Memory without organization: properties of a model with random storage and undirected retrieval, Cogn. Psychol. 7 (1975) 495–531.


