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Research report

Behavioural and neural evidence for the impact of fluency context on conscious memory

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ABSTRACT

It has been recently suggested that fluency may impact recognition memory performance when the fluency context varies from trial-to-trial. Surprisingly, such an effect has proved difficult to detect in the masked priming paradigm, one of the most popular means to increase fluency-based memory judgements. We conducted a functional magnetic resonance imaging (fMRI) experiment in which participants encoded words at study and, at test, performed a recognition memory task within a masked priming procedure. In order to optimise the chances of finding priming effects on recognition memory performance, we used low-frequency words, which have been shown to increase hits relative to false alarms and enhance masked priming effects. Fluency context was manipulated by either mixing primed and unprimed trials [Random context (RC) experiment] or blocking primed and unprimed trials [Blocked context (BC) experiment]. Behaviourally, priming affected high-confidence memory performance only in the RC experiment. This behavioural effect correlated positively with neural priming in several recognition memory regions. Moreover, we observed a functional coupling between the left middle temporal gyrus and the left parietal and posterior cingulate cortices that was greater for primed relative to unprimed words. In contrast, in the BC experiment, despite similar activity in recognition-memory-related regions, we did not find any significant correlations between neural and behavioural priming. Finally, we observed striking differences in the neural correlates of masked priming between the RC and BC experiments not only in location but also in direction of the neural response. Possible implications of these findings are discussed.

1. Introduction

Within dual-process frameworks, recognition memory decisions can be based on two distinct kinds of memory: familiarity and recollection. Familiarity is often described as a fast-acting and relatively automatic process, whereas recollection is believed to be an all-or-none threshold process, in which contextual information associated with the encoding of an item is retrieved in addition to the memory for the item

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itself (e.g., Mandler, 1980; Mayes, Montaldi, & Migo, 2007; Yonelinas, 1994).

The seminal work of Jacoby and colleagues (e.g., Jacoby & Dallas, 1981; Jacoby & Whitehouse, 1989) showed that recognition memory judgements can also sometimes be based on the relative ease with which an item is processed. Several lines of evidence seem to converge on the idea that fluently-processed items are more likely to be endorsed as "old" regardless of the item's true study status, leading to illusions of recognition (e.g., Jacoby & Whitehouse, 1989; Whittlesea, 1993; Whittlesea, Jacoby, & Girard, 1990). Within the recognition memory context, the masked priming paradigm has particularly stood out as a powerful means to artificially enhance fluency. In this procedure, participants make recognition judgements on test items that are preceded by brief and masked presentations of the same (primed) or different (unprimed) item, effectively preventing any conscious identification of these items (also called "primes"). Typically, the probability of making an "old" judgement to the test item (e.g., "sugar") is increased when preceded by a matched prime (e.g., "sugar") than by a non-matched prime (e.g., "lamp") (e.g., Jacoby & Whitehouse, 1989; Rajaram & Roediger, 1993; Westerman, Lloyd, & Miller, 2002).

Early manipulations of fluency during recognition memory tests were shown to affect familiarity but not recollection (e.g., Kinoshita, 1997; Rajaram & Geraci, 2000; Rajaram, 1993). These studies employed a Remember/Know (R/K) procedure which provides rough estimates of familiarity (K responses) and recollection (R responses), and showed that the bias to respond "old" was only observed when recognition judgements were subsequently associated with a K response. These behavioural data linking fluency and familiarity have been also supported by research using event-related potentials (ERPs) (e.g., Leynes & Zish, 2012; Taylor & Henson, 2012; Wolk et al., 2004; Woollams, Taylor, Karayanidis, & Henson, 2008), and, more recently, functional magnetic resonance imaging (fMRI) (e.g., Dew & Cabeza, 2013). In Dew and Cabeza's fMRI study, a masked priming paradigm was used in the scanner and the authors showed that activity in the perirhinal cortex was reduced for primed false alarms (i.e., unstudied items incorrectly given an "old" response) relative to both unprimed false alarms and primed/unprimed correct rejections (i.e., unstudied items correctly given a "new" response). Moreover, the degree of attenuation of perirhinal activation was negatively correlated with the behavioural tendency to call an item "old". The observation that activity in the perirhinal cortex is modulated by fluency for new, unstudied items is remarkable, especially given the abundant evidence linking perirhinal cortex reductions to objective familiarity memory. Dew and Cabeza concluded that perirhinal activity reductions found for false alarms may reflect fluency rather than familiarity memory per se, because there could not have been objective memory for false alarms since the words had not been studied before.

Some recent studies, however, have also indicated that recollection memory may be as susceptible to fluency manipulations as familiarity (e.g., Kurilla & Westerman, 2008; Taylor & Henson, 2012; Wang, Li, Gao, Xu, & Guo, 2015). For example, Taylor and Henson (2012) used a modified masked priming procedure and showed that when previously studied test targets (e.g., guitar) were preceded by conceptually-related masked primes (e.g., piano), the incidence of R responses was increased relative to when prime and target were the same word. The authors speculated that because the study task involved a high degree of elaboration, the concept of the prime could have possibly been one of the concepts spontaneously generated during the study phase; the combined activation of the prime and target may have increased the probability of retrieval of the entire episodic trace, resulting in recollection. Their interpretation was supported by a subsequent fMRI study in which activity in recollection-related parietal structures correlated with the size of the behavioural priming effect (Taylor, Buratto, & Henson, 2013). Importantly, the increase in R judgements following priming occurred for hits but not for false alarms. This further indicated that priming increased retrieval of internal source information, rather than leading to an illusory feeling of memory as occurs with fluency-driven familiarity (which tends to increase both hits and false alarms to a similar level).

Regardless of whether fluency affects familiarity, recollection, or both, it has been argued that reliance on fluency during recognition memory judgements is largely dependent on the level of fluency associated with the surrounding stimuli. For example, Westerman (2008) observed that participants were more likely to respond "old" in contexts in which only a few items were primed relative to when, for example, all items had been primed. The finding that an increase in "old" responding is only detectable when the fluency context includes sparse primed items at test led Leynes and Zish (2012) to investigate the role of fluency context during recognition memory. They presented a series of words at study and participants were asked to count the number of vowels in each word. Later, at test, ERPs were recorded while participants engaged in a recognition memory test for old and new words, half of which were presented slightly blurred whereas the other half were presented in a clear typeface. Critically, the authors manipulated fluency context by testing a group of participants for whom clarity was varied randomly, and a separate group for whom blurry and clear words were presented in separate blocks. The results indicated that recognition memory accuracy was higher for clear than blurry words when clarity was varied randomly, whereas accuracy was equivalent when clear and blurry words were blocked. Furthermore, blocking clarity revealed a posterior negative ERP component (280–400 msec) that was sensitive to both old/new and clear/blurry. Conversely, when clarity was randomised across trials, repetition influenced the FN400, a putative ERP correlate of familiarity (Mecklinger, 2000), but not the earlier posterior negativity. The authors concluded that recognition was supported by familiarity when clarity varied randomly, whereas it was based on repetition fluency when clarity was blocked. They speculated that repetition fluency (old *vs* new words) combined with perceptual fluency (clear *vs* blurry words), and the mixing of these fluency signals (old and clear) made those items stand out relative to the surrounding items, leading to feelings of familiarity (see also Bruett & Leynes, 2015). Importantly, this effect could only occur when the context allowed for variations in fluency levels, since assessing whether a word is fluent requires some type of benchmark.

2. The present study

The present study had three main aims. First, we wished to determine whether recognition memory performance could be affected by a masked priming manipulation in an fMRI environment (Experiment 1). Despite Leynes and Zish's impressive demonstration of the impact of fluency context on recognition memory accuracy, enhanced recognition memory performance through masked repetition priming has proved elusive. The reason for this is unclear. It seems evident however, that in order to detect any effect of priming on recognition memory performance, it is critical to use a manipulation that allows priming to selectively increase the proportion of hits but not false alarms. For that purpose, we used low-frequency (LF) words during a masked repetition priming paradigm. Memory studies have shown that LF words have higher hit rates as well as lower false alarm rates than high-frequency words (Glanzer & Adams, 1990), regardless of whether words are studied in either pure or mixed lists (e.g., Clark & Burchett, 1994). It has been suggested that this LF-word advantage comes about due to the memory representations of LF words being more distinct than their high-frequency counterpart (Shiffrin & Steyvers, 1997), leading to greater remembering of those words. Moreover, and importantly, the magnitude of masked priming effects also seems to be larger for LF than high-frequency words (e.g., Bodner & Masson, 2001). Thus, we reasoned that a manipulation that strongly affects both hits and primed words would be conducive to a situation in which objective recognition memory could be enhanced through priming. In other words, we expected a greater influence of priming on hits relative to false alarms, which would increase overall recognition memory accuracy for the primed condition.

At the neural level, we expected behavioural priming (i.e., difference in recognition accuracy between primed and unprimed trials) to correlate with neural priming (i.e., difference in the parameter estimates between unprimed and primed hits) in brain regions typically involved in recognition memory, such as the left parietal cortex, posterior cingulate/retrosplenial cortex and hippocampus (e.g., Rugg & Vilberg, 2013; Taylor et al., 2013). Given that repetition might decrease activity for primed relative to unprimed hits in neocortical regions, it is possible that this activity may then be transmitted to higher-level recognition memory regions (see Gagnepain et al., 2011 for a similar argument). If so, we would expect a positive correlation between behavioural priming (primed minus unprimed) and neural priming (unprimed minus primed). Furthermore, given the pervasiveness of the left middle temporal gyrus (MTG) in subliminal priming studies (e.g., Nakamura, Dehaene, Jobert, Le Bihan, & Kouider, 2005, 2007), as well as its functional connectivity with other recognition memory sites during implicit memory tasks (Gagnepain et al., 2011; Wig, Buckner, & Schacter, 2009), we also predicted that left MTG would show greater functional connectivity with recognition memory brain regions for primed versus unprimed trials.

The second aim of the present study was to explore the impact of fluency context on conscious memory using a manipulation similar to the one used by Leynes and Zish. Whereas in Experiment 1 primed and unprimed trials were randomly interspersed [Random context (RC) experiment], in Experiment 2, primed and unprimed trials were grouped into two distinct blocks [Blocked context (BC) experiment]. We predicted that, during the RC experiment, the different fluency cues (i.e., fluency derived from the masked priming manipulation and fluency derived from the study phase) would likely combine to produce an enhanced memory signal, leading to successful recognition memory. In contrast, during the BC experiment, the unchanging nature of the fluency context would be a poor basis for fluency-based decisions, so we predicted that recognition memory performance would not be influenced by priming. At the neural level, we expected a similar pattern of brain activations between the RC and BC experiments during objective recognition memory. Contrary to the RC experiment predictions however, we did not expect brain-behaviour correlations in the recognition memory regions during the BC experiment because recognition memory should not be influenced by priming when the fluency context is unchanging.

Finally, Leynes and Zish also observed that the RC versus BC manipulation generated distinct ERP effects in both time (280–400 msec and 400–600 msec for BC and RC respectively) and location (parietal and mid-frontal topography for BC and RC respectively). Thus, we sought to explore the source of these electrophysiological effects more precisely using fMRI. For that aim, we contrasted primed versus unprimed words, collapsed across response category and confidence level (see Methods), in order to determine whether fluency context would also affect the BOLD response, regarding direction and/or location of activation.

3. Methods

3.1. *Participants*

Forty-eight (24 in each experiment) right-handed undergraduate students of the Saarland University were recruited ($M = 23.33$ years, $SD = 4.86$ years) in exchange for monetary compensation and/or course credit. All participants had normal or corrected-to-normal vision with no history of psychiatric or neurological disorders. All gave informed written consent to take part in this study before the start of the experiment in accordance with the ethical approval obtained from the ethic committee of the Faculty of Empirical Human Science of the Saarland University. Five participants (two from the RC experiment and three from the BC experiment) were excluded due to a technical error. A further participant from the RC experiment was also excluded due to very poor performance (below chance levels) in all conditions.

3.2. *Materials*

Six-hundred German low-frequency words were selected from the database Celex (http://celex.mpi.nl/). Three lists were created, each containing 200 words. These lists were subsequently divided into two sub-lists of 100 words each. The resulting six sub-lists were matched in terms of word frequency (mean frequency: 1.63 per million; range: 1.54–1.73), word length (mean: 5.77 letters; range: 4–7), number of vowels (mean:

2.19 vowels; range: 1–4) and word class (each sub-list contained 25 verbs, 25 adjectives and 50 nouns). In addition, care was taken that, within each list, the words in one sub-list were completely unrelated to the words of its associated sub-list.

Two of the three lists were selected to form unprimed prime/test combinations, which were created by using the words of one sub-list as primes and the other as targets. One of these lists was assigned to the studied condition, whereas the other list was assigned to the unstudied condition. The remaining list was used to create primed prime/target combinations. Because primes and targets for primed trials are essentially the same word, one of the sub-lists was assigned to the studied condition, whereas the other sub-list was assigned to the unstudied condition. Thus, in the end, there were 200 primed prime/target and 200 unprimed prime/target trials. The assignment of the lists and sub-lists to the experimental conditions was done in a fully counterbalanced manner across participants.

3.3. *Procedure*

The entire experiment consisted of two study–test–rest cycles. Participants laid in the scanner during the whole experiment, and fMRI data was collected within each of these periods (only the test phase data is reported here). Prior to entering the scanner, participants were told that they would see a series of German words on the projector screen, and that they should decide whether each word either contained exactly two vowels or more/less than two vowels by pressing one of two buttons.

Because precise timing was crucial in our experiment, timing parameters were defined as frames-per-second in the programme controlling the stimulus presentation. However, for the sake of clarity, we describe the timings in milliseconds, noting that 1000 msec correspond to 60 frames. Each experimental study trial started with a fixation cross displayed for 2700, 2900, 3100 or 3300 msec selected from a random uniform distribution. This was followed by the presentation of a word in uppercase letters for 1000 msec. A total of 100 words were presented within each study phase session, which lasted approximately 5 min to complete.

The test phase immediately followed the study phase. Participants saw 100 studied and 100 unstudied (new) words and were asked, first, to decide whether a word was old or new and, second, to choose among four choices how confident they were that the word was old/new (the first and second choices corresponded to low confidence levels; the third and fourth choices corresponded to high confidence levels[1]). Participants were also made aware of the different types of recognition memory they could experience in this study (i.e., familiarity and recollection).

The test procedure followed that of Taylor and Henson's (2012) very closely. Each test trial commenced with a fixation cross presented centrally on the projector screen for one of the values taken from a random uniform distribution (400, 600, 800 or 1000 msec). This was followed by the presentation of a mask, consisting of seven hash (#) symbols flanked by a less than (<) and greater than (>) symbol, for 500 msec. A prime word was then presented for 50 msec, followed by another mask consisting of seven symbols (%&$€@§?), presented for 50 msec. The test word was then shown for 300 msec and followed by a blank screen for 2000 msec, within which time participants made their old/new decisions. Finally, a screen containing the four confidence choices was shown for 3000 msec.

The 48 participants were randomly assigned to either the RC (Experiment 1) or the BC (Experiment 2) experiment. For the RC experiment, primed trials were randomly intermixed with unprimed trials, whereas for the BC experiment, primed and unprimed trials were grouped in two separate blocks (i.e., one block with only primed words and another block with only unprimed words; the order of the blocks was counterbalanced across participants).

After participants completed the experiment, we administered a funnelled debriefing procedure outside the scanner (subjective test of awareness). We began by asking participants general questions about the experiment such as "Did you notice anything particular during the experiment?" that led to increasingly more specific ones such as "Did you notice any words appearing very briefly between masks?". Furthermore, in order to obtain an objective index of prime awareness, we also administered a test in which we instructed participants to report with a key press whenever they detected a word flashed within the two masks. "Prime" trials (i.e., trials in which a word was presented between the masks) were randomly intermixed with "non-prime" trials (i.e., trials in which a random string of symbols was presented between masks). We used exactly the same parameters as in the real experiment, with the only difference that the target word was replaced by a random string of letters. This was necessary because, if participants were indeed completely unaware of the prime, showing a real word as target could bias participants to give that word as a response (regardless of whether the target word was the same as, or different from, the prime). Thus, presenting a random string of letters prevents any biases and maintains the same visual input as in the real experiment.

The whole experiment was programmed and responses collected using the software Psychopy (http://www.psychopy.org/).

3.4. *Design*

For each experiment (i.e., RC and BC), the behavioural analysis focused on accuracy (i.e., proportion of correct responses) and reaction times (RTs) as the dependent variables. Because there were an insufficient number of trials in some confidence levels for certain response categories (e.g., 4-choice false alarms), and because that would have prevented us from using the same design matrix for every participant, we collapsed the 1 and 2 choices into a low confidence (LC) category, and the 3 and 4 choices into a high confidence (HC) condition. Thus, the experimental design consisted of category (hits [Hs], misses [Ms], false alarms [FAs], correct rejections [CRs]), prime status (primed, unprimed) and confidence (HC, LC) as within-subject factors. The data were analysed using repeated-measures Analysis of Variance (ANOVA) and paired *t*-tests. A Huynh-Feldt correction was applied to the degrees of freedom of those tests for which the assumption of sphericity was

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[1] Each confidence choice was given a label (1: Guess, 2: Not sure, 3: Sure, 4: Know) as we found that these labels were more informative to participants than simply numbers.

violated. The alpha level was set, for all statistical tests, at .05 and *t*-tests were two-tailed. However, we used a one-tailed *t*-test for comparisons involving prime status, as there was no reason to expect unprimed words to show increased fluency relative to primed ones.

3.5. *MR image acquisition*

The fMRI data were collected on a 3T Siemens Skyra MRI scanner using a gradient-echo echo planar imaging sequence, providing Blood Oxygen Level Dependent (BOLD) contrast, with parameters as follow: TR = 1.8 sec, TE = 35 msec, flip angle = 75°, FOV = 240 × 240 mm^2, and matrix size = 96 × 96, voxel resolution = 3 × 3 × 3.75 mm^3. The whole brain was covered with 32 contiguous axial slices, positioned parallel to the AC-PC axis, acquired in ascending order. A high-resolution structural T1-weighted image was also acquired for each participant (voxel resolution = .9375 × 1.1733 × .90 mm^3).

3.6. *fMRI analysis*

Imaging data were analysed using the Statistical Parametric Mapping (SPM8, http://www.fil.ion.ucl.ac.uk/spm/) toolbox. Prior to any preprocessing of the images, the origin of each scan was manually set to match the anterior commissure and the image rotated to be better aligned with the MNI space. Then, the images were subjected to preprocessing, which included: spatial realignment to correct for movement; slice timing correction (using the middle slice as the reference slice); co-registration of the structural image to the mean EPI across the realigned volumes; segmentation of the structural image into grey matter, white matter and cerebrospinal fluid; normalisation of the EPI images into MNI space; and spatial smoothing of the normalised images using an isotropic Gaussian kernel with a full-width at half-maximum (FWHW) of 6 mm (final smoothness approximately 11 × 11 × 11 mm).

Statistical analysis of the fMRI data was performed in two separate stages. In the first stage, the BOLD response to each event-type was modelled by convolving a series of delta functions at stimulus onset with a canonical haemodynamic response function. A participant-specific general linear model (GLM) was created for each test session, including eight regressors representing the events of interest (Category × Priming; see Table 1 for the proportion of responses) as well as three additional regressors for the discarded trials, the confidence choices period and baseline effects. The GLM also included six regressors representing the movement parameters (3 translations and 3 rotations), estimated during realignment, as nuisance regressors for each session, to account for residual artefacts after realignment. A high-pass filter with a cut-off of 128 sec was used to remove low-frequency drifts, and temporal autocorrelation across scans was accounted for using an autoregressive AR (1) model. Parameter estimates were obtained for each event of interest by fitting the GLM to the data. Images of contrasts, individually masked by the grey matter mask created during segmentation, were computed for each parameter estimate weighted across each of the two sessions.

In the second-stage model the contrast images that resulted from the first-level analysis of each participant's data were entered into a GLM, treating participants as a random effect. Statistical parametric maps (SPM's) of the *F*- or *t*-statistic were generated for the various contrasts of interest. All whole-brain SPM's were initially thresholded at an uncorrected $p < .001$. In order to control for Type I errors, a cluster-wise threshold of $p < .05$, corrected for multiple comparisons, was determined for the whole-brain analyses. This threshold was set at a 26-voxel extent as estimated using a Monte Carlo simulation (1000 iterations) implemented in the AlphaSim routine of the software package AFNI. Linear correlational analyses between the mean parameter estimates for the contrast primed versus unprimed HC Hs and the mean individual behavioural performance were also performed.[2]

When appropriate, region-of-interest (ROI) analysis were also performed using a priori regions identified in previous studies. The signal associated with each contrast was computed and averaged across the relevant ROI using in-house Matlab functions and subsequently submitted to repeated-measures ANOVAs. Whenever *t*-tests were performed, the alpha level was set to .05. In addition, small volume corrections (SVC) within the hippocampus were also conducted using anatomical ROIs based on structural probability maps of the left and right hippocampus included in the Anatomy toolbox (Eickhoff et al., 2005).

Finally, we used Psychophysiological interactions (PPI) to estimate connectivity between a source (left middle temporal gyrus – MTG) and two recognition memory regions (left parietal cortex and posterior cingulate cortex) that have been linked to successful memory retrieval during masked priming (Taylor et al., 2013) and were also identified in our whole-brain recognition contrast. The reason for selecting the left MTG as a seed region was because changes in activation within this region have been consistently detected in subliminal word priming studies (e.g., Nakamura et al., 2005, 2007), which may relate to the presumptive role of this region in the storage and access of lexical representations (Lau, Phillips, & Poeppel, 2008). Furthermore, connectivity between the left MTG and other cortical and subcortical regions has been observed in some memory tasks (e.g., Gagnepain et al., 2011; Takahashi, Ohki, & Kim, 2008; Wig et al., 2009), and transcranial magnetic stimulation (TMS) applied to the left temporal cortex disrupted subliminal word priming during a lexical decision task (Nakamura et al., 2006).

We used a generalized form of context-dependent psychophysiological interaction analysis (gPPI; McLaren, Ries, Xu, & Johnson, 2012). At first level, we included 1) the relevant task regressors corresponding to the psychological variables of interest (as in the whole-brain analysis), 2) the time course data of the source region (physiological variable), derived by extracting the first eigenvariate from a sphere of 20 mm radius centred around the coordinates of the relevant ROI detected at the group level, and 3) the critical cross-products between the psychological variables and physiological variable (the PPI term). For the second level analysis, the PPI contrast images generated at first level were entered into a GLM and one-

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[2] Extreme responses (more than 3 standard deviations above or below the mean value) were excluded from this analysis, as we were concerned that they could potentially bias correlations in an unusual way.

sample *t*-tests carried out. Multiple comparisons were corrected using 1000 Monte Carlo simulations (corrected threshold: $p < .05$, cluster size: 10 contiguous voxels).

4. Results

We present the behavioural analyses first, followed by the fMRI analyses. Given that the data were collected in two separate studies, and in keeping with studies that used a similar fluency context manipulation (Leynes & Zish, 2012; Westerman, 2008), the data were analysed separately for each type of context. However, we also performed inter-experimental analyses using fluency context (RC *vs* BC) as a between-subjects factor, in order to examine differences directly between the two types of context.

4.1. *Behavioural results*

4.1.1. *Experiment 1 (RC experiment)*

Table 1 shows the mean proportion of responses in each category (Hs, Ms, FAs, CRs) for each context (RC, BC), as a function of confidence level (HC, LC) and prime status (primed and unprimed).

An initial paired *t*-test was conducted on the Pr scores (Hs minus FAs) for primed and unprimed trials, collapsed across confidence level. This test was significant, $t(20) = 2.30$, $p < .05$, $d = .50$, indicating more accurate recognition memory for primed (.39) relative to unprimed (.36) trials.

Next, we examined whether this fluency effect was specific to a particular confidence group by conducting a 2 Prime Status (primed, unprimed) × 2 Confidence (HC, LC) repeated-measures ANOVA. The main effect of prime status approached significance, $F(1,20) = 3.94$, $p = .06$, $\eta^2_p = .16$, replicating the test above. The main effect of confidence was significant, $F(1,20) = 79.75$, $p < .001$, $\eta^2_p = .80$, with more accurate recognition memory for HC (.37) than LC (−.002) trials. There was also a trend for a Prime × Confidence interaction, $F(1,20) = 3.95$, $p = .06$, $\eta^2_p = .17$, suggesting that priming increased HC recognition memory, $t(20) = 2.40$, $p < .05$, $d = .57$, but not LC recognition memory, $t(20) = -.50$, $p > .10$, $d = .10$. Because of our particular interest in successful recognition memory, we restricted further analyses to HC data only, as it appeared that LC memory was at chance level.

Given that any increase in recognition memory accuracy in the HC condition must stem from a disproportionate increase of HC Hs relative to HC FAs, we predicted that priming would affect Hs to a greater extent than FAs in the HC condition. A 2 Category (Hs, FAs) × 2 Prime Status (Primed, Unprimed) repeated-measures ANOVA for HC trials yielded main effects of category, $F(1,20) = 105.50$, $p < .001$, $\eta^2_p = .84$, and prime status, $F(1,20) = 4.96$, $p < .05$, $\eta^2_p = .20$. Importantly, these main effects were qualified by a significant Category × Prime status interaction, $F(1,20) = 5.77$, $p < .05$, $\eta^2_p = .22$. As predicted, priming increased the incidence of Hs, $t(20) = 2.82$, $p < .01$, $d = .62$, but not FAs, $t(20) = -.62$, $p > .10$, $d = .01$.

Regarding reaction times (RTs), a 4 Category (Hs, Ms, FAs, CRs) × 2 Prime Status (primed, unprimed) repeated-measures ANOVA on the HC data only revealed a significant main effect of prime status, $F(1,17) = 9.58$, $p < .01$, $\eta^2_p = .36$, with faster RTs for primed (1243 msec) relative to unprimed (1279 msec) words.

4.1.2. *Experiment 2 (BC experiment)*

Contrary to the RC experiment, there was no evidence that priming increased Pr when trials were collapsed across confidence level in the BC experiment, $t(20) = -.29$, $p > .10$, $d = .06$. In fact, recognition accuracy for primed trials (.35) was (non-significantly) lower than recognition memory for unprimed trials (.36), which stands in contrast to the positive difference found in the RC experiment. When the data were further separated into confidence levels, a 2 Prime Status (primed, unprimed) × 2 Confidence (HC, LC) repeated-measures ANOVA only revealed a main effect of confidence,

Table 1 – Mean proportion of responses and reaction times (RTs) for all response categories, as well as Pr scores (hits minus false alarms), for the Random and Blocked context experiments, separated by confidence level and prime status. Hs = hits, Ms = misses, FAs = false alarms, CRs = correct rejections. HC = high confidence, LC = low confidence. Standard error of the mean is given within parentheses.

	Random					Blocked				
	Hs	Ms	FAs	CRs	PR	Hs	Ms	FAs	CRs	PR
Proportion										
HC										
Primed	.47 (.04)	.08 (.01)	.09 (.01)	.37 (.03)	.39 (.03)	.43 (.03)	.14 (.02)	.11 (.02)	.41 (.03)	.32 (.03)
Unprimed	.44 (.04)	.11 (.01)	.09 (.01)	.38 (.03)	.35 (.04)	.41 (.03)	.15 (.02)	.10 (.01)	.40 (.04)	.30 (.03)
LC										
Primed	.18 (.01)	.19 (.02)	.18 (.03)	.30 (.02)	−.004 (.03)	.17 (.02)	.16 (.02)	.14 (.02)	.24 (.03)	.02 (.01)
Unprimed	.17 (.01)	.21 (.02)	.17 (.03)	.29 (.03)	.001 (.03)	.16 (.02)	.18 (.02)	.11 (.01)	.27 (.03)	.04 (.01)
RTs										
HC										
Primed	1160 (50)	1269 (40)	1238 (63)	1204 (34)		1255 (54)	1397 (60)	1368 (75)	1334 (55)	
Unprimed	1190 (49)	1263 (37)	1330 (71)	1242 (37)		1257 (47)	1418 (58)	1403 (67)	1341 (54)	
LC										
Primed	1339 (43)	1310 (39)	1342 (53)	1361 (39)		1474 (64)	1490 (54)	1509 (66)	1492 (54)	
Unprimed	1364 (60)	1369 (43)	1351 (61)	1379 (46)		1488 (57)	1473 (53)	1467 (64)	1472 (53)	

Note: Proportions may not add up to 1 due to trials in which no response was given.

$F(1,20) = 83.84$, $p < .05$, $\eta^2_p = .81$, with more accurate recognition memory for HC (.31) than LC (.03) trials. Neither the main effect of priming, $F(1,20) = .06$, $p > .10$, $\eta^2_p = .003$, nor the interaction, $F(1,20) = 2.13$, $p > .10$, $\eta^2_p = .10$, approached significance.

As with the RC experiment, a 2 Category (Hs, FAs) × 2 Prime Status (primed, unprimed) repeated-measures ANOVA was conducted for HC trials only. This revealed a significant main effect of category, $F(1,20) = 124.13$, $p < .001$, $\eta^2_p = .86$, reflecting the larger proportion of Hs than FAs. However, neither the main effect of prime status, $F(1,20) = 1.29$, $p > .10$, $\eta^2_p = .06$, nor the interaction, $F(1,20) = .52$, $p > .10$, $\eta^2_p = .03$, reached significance.

Regarding RTs, a 4 Category (Hs, Ms, FAs, CRs) × 2 Prime Status (primed, unprimed) repeated-measures ANOVA on the HC data only revealed a significant main effect of category, $F(1,60) = 17.10$, $p < .001$, $\eta^2_p = .46$, with faster RTs for Hs (1326 msec) and FAs (1351 msec) relative to both Ms (1482 msec) and CRs (1500 msec). Importantly, the main effect of priming was non-significant, $F(1,20) = .39$, $p > .10$, $\eta^2_p = .04$, suggesting that, as with recognition accuracy, blocking primes disrupts RT-based fluency.

4.1.3. *Interexperimental analyses*

There was a trend for a greater recognition memory difference (i.e., primed Pr minus unprimed Pr) in the RC relative to the BC, $t(32.52) = 1.42$, $p = .08$, $d = .44$. However, a 2 Context (RC, BC) × 2 Category (Hs, FAs) × 2 Prime Status (primed, unprimed) mixed repeated-measures ANOVA did not reveal any interactions with the context factor (all $Fs < 1.53$, $ps > .10$).

For the RT data, a 2 Context × 2 Prime Status × 4 Category (Hs, Ms, FAs, CRs) mixed repeated-measures ANOVA revealed a significant Prime Status × Context interaction, $F(3,2.44) = 5.63$, $p < .01$, $\eta^2_p = .13$, indicating faster RTs for primed versus unprimed trials in the RC relative to the BC.

4.1.4. *Subjective and objective awareness measures*

For the subjective measure of prime awareness (funnelled debriefing procedure), none of the participants tested reported having noticed the primes, or that anything at all appeared other than the stimuli presented supraliminally. For the objective test of prime awareness, we conducted a one-sample *t*-test for each context type to explore whether participants would still perform above chance at identifying the prime words. For participants in both context types, accuracy in identifying whether or not a word had been presented was at chance [RC: $t(17) = .75$, $p > .10$, $d = .17$; BC: $t(21) = -.17$, $p > .10$, $d = .03$]. Furthermore, the participants that claimed to have seen something were not able to name the correct word. Note that this happened even though we maximised the chances of detecting the primes. This is because, for the objective measure test of prime awareness, we informed participants that a prime would occasionally be presented and asked them to direct their full attention to it, as opposed to not informing participants at all about the prime, as in the real experiment. Thus, these results convincingly demonstrate that participants were unaware of the primes during the test phase, and that the impact priming had on behavioural performance cannot be accounted for by differences in participants' conscious behaviour between primed and unprimed words.

4.1.5. *Summary of behavioural data*

For the RC experiment, recognition memory accuracy was higher for primed relative to unprimed words and this effect was only observed for HC trials, suggesting that priming influenced HC recognition memory. As predicted, this increase in recognition accuracy for HC trials resulted from a selective increase in Hs without changing FAs. Contrary to the RC experiment, there was no evidence that priming affected HC trials in the BC experiment. Priming also led to faster RTs in the RC experiment, but had no effect on RTs in the BC experiment. Finally, subjective and objective prime detection measures indicated that participants were unaware of the primes in this study.

4.1.6. *fMRI results*

As with the behavioural data, the imaging data were initially analysed separately for each experiment. The general analysis strategy consisted of examining the effects of interest collapsed across the confidence factor so as to benefit from the greater amount of trials per event included in the design matrix. For the whole-brain analysis, we did not include the confidence factor because some participants had very few trials in certain event types (e.g., unprimed HC FAs) to get reliable parameter estimates. Furthermore, there were a few participants without valid trials in certain response categories, which would have prevented us from using the same factorial design for all participants, and would, thus, require separate models. Nevertheless, we also conducted a separate GLM analysis with the confidence factor by analysing only those participants which had non-zero events in all response categories for both confidence levels (three participants excluded in the RC experiment, one participant excluded in the BC experiment). This was done in order to be able to extract parameter estimates for primed and unprimed HC Hs which were used for computing correlations between behavioural and neural priming.

4.1.7. *Experiment 1 (RC experiment)*

We initially ran a whole-brain analysis using category (Hs, Ms, FAs, CRs) and prime status (primed, unprimed) collapsed across confidence level. We began with the identification of regions associated with general successful recognition memory by conducting a simple contrast that searched for voxels showing greater activity for Hs relative to Ms (see Prince, Daselaar, & Cabeza, 2005; Quamme, Weiss, & Norman, 2010, for a similar approach).

Fig. 1 and Table 2 show the results of this contrast, which revealed large activation clusters in occipital, parietal and frontal regions. Importantly, increased activity for Hs relative to Ms was observed in the left parietal cortex (particularly in the angular gyrus and intraparietal sulcus), left precentral gyrus, left MTG and posterior cingulate cortex, brain regions commonly associated with successful recognition memory (e.g., Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Rugg & Vilberg, 2013; Vilberg & Rugg, 2007, 2012; Yonelinas, Otten, Shaw, & Rugg, 2005).

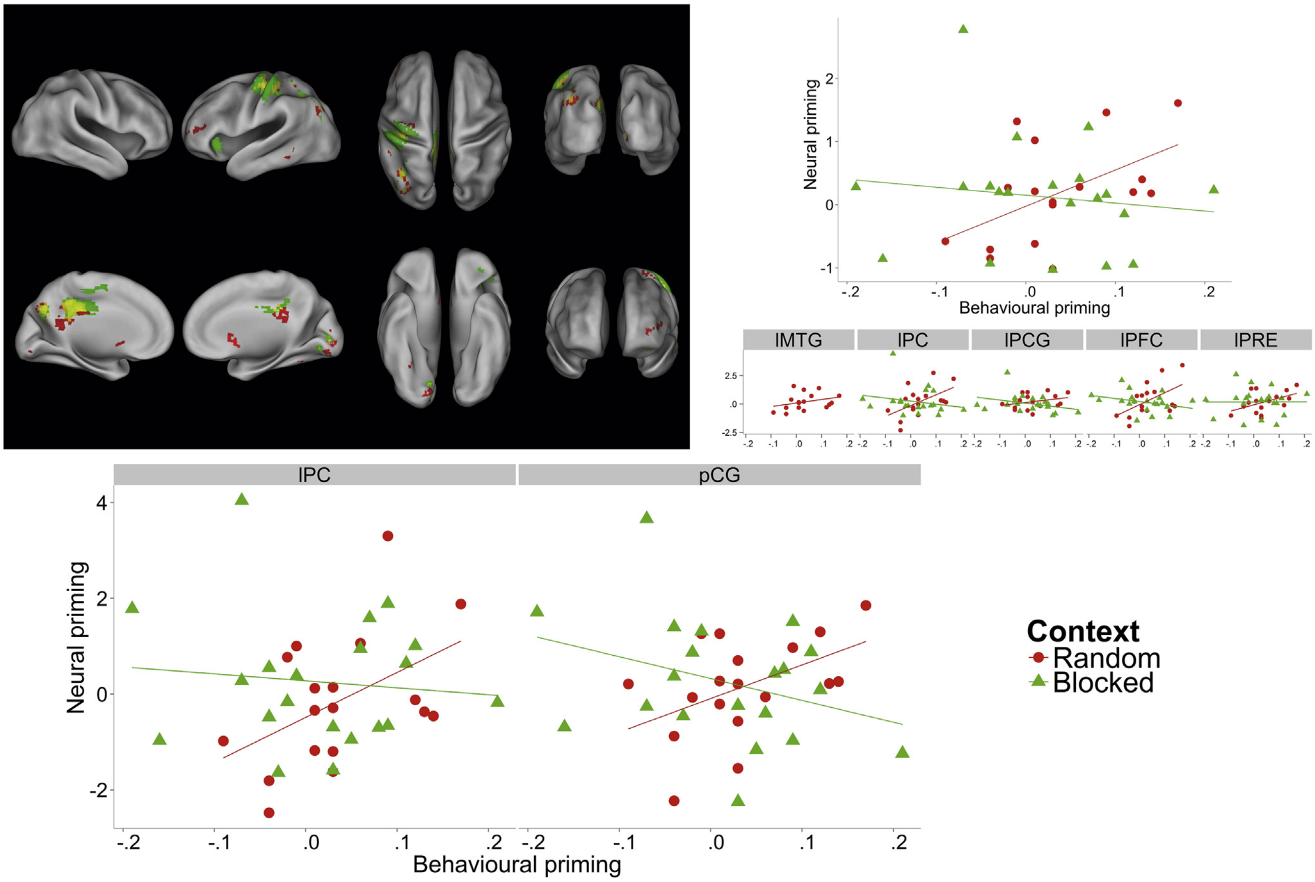

Fig. 1 – Results of the Hs-Ms whole-brain contrast. Top left: Surface rendering of regions showing increased activity for Hs relative to Ms during the Random (red) and Blocked (green) context experiments. Yellow indicates overlap between the two experiments. Top right: Correlation between neural priming (unprimed minus primed HC Hs) in five recollection regions, and behavioural priming, calculated as the difference in recognition memory accuracy between primed and unprimed trials (top: overall correlation for all five regions, bottom: correlation for each separate region). Bottom: Similar brain-behaviour correlations were also identified in two regions based on the coordinates of the left parietal and posterior cingulate cortices in Taylor et al.'s (2013) study. lMTG = left middle temporal gyrus; lPC = left parietal cortex; lPFC = left prefrontal cortex; lPRE = left precentral gyrus; lPCG = left posterior cingulate gyrus.

Table 2 – Brain regions exhibiting increased activation for Hs versus Ms in the Random (top) and Blocked (bottom) context experiments. Approximate Brodmann areas (BA) are given in parentheses. L = Left, R = Right.

Region	Voxels	MNI coordinates			Z-scores
		x	y	z	
Random					
L precentral gyrus (BA 4,6)	187	−36	−19	55	4.99
L inferior parietal cortex (BA 39,40)	129	−33	−70	37	4.61
R lingual gyrus (BA 18)	131	9	−82	−14	4.39
L/R caudate	45	6	14	−2	4.39
L middle temporal gyrus (BA 21)	30	−57	−37	−11	4.17
R cerebellum	68	27	−52	−20	4.09
L precuneus (BA 7)	63	−12	−64	28	4.00
L/R mid-posterior cingulate cortex (BA 31)	187	−6	−40	37	3.97
L mid-inferior frontal gyrus (BA 10,46)	32	−33	53	4	3.91
Blocked					
L precentral gyrus (BA 4,6)	491	−39	−25	67	5.49
L precuneus (BA 31)	89	−6	−67	34	5.31
L/R mid-posterior cingulate cortex (BA 31)	255	−3	−37	37	5.18
L inferior frontal gyrus (BA 47)	79	−33	23	−5	4.84
R lingual gyrus (BA 18)	52	15	−76	−2	4.75
L inferior parietal cortex (BA 39,40)	92	−36	−70	37	4.10

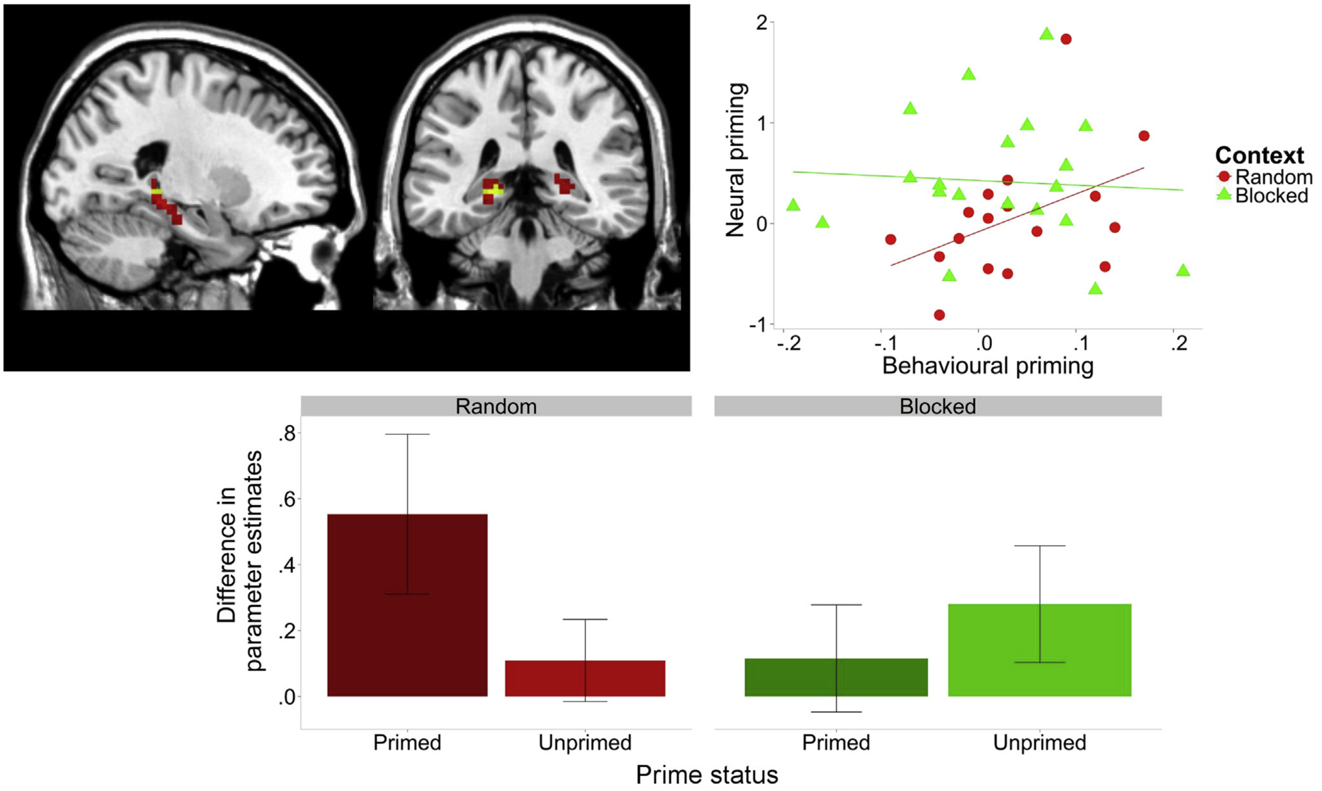

Fig. 2 – Results of the SVC in the hippocampus. Top left: Location of the hippocampal region showing increased activity for Hs relative to Ms during the Random (red) and Blocked (green) context experiments. Yellow indicates overlap between the two experiments. Top right: Correlation between neural priming (unprimed minus primed HC Hs) in the hippocampus and behavioural priming, calculated as the difference in recognition memory accuracy between primed and unprimed HC trials. Bottom: Average parameter estimates for the Hs-Ms difference within the hippocampus for the Random (red) and Blocked (green) context experiments.

Because the behavioural data suggested that priming only affected recognition for HC trials, we decided to conduct simple correlations between neural priming for HC Hs (i.e., unprimed HC Hs minus primed HC Hs) averaged among the recognition memory regions (i.e., left parietal cortex, left precentral gyrus, left inferior prefrontal cortex, posterior cingulate cortex, left MTG), and behavioural priming (calculated as the difference in recognition memory performance between primed and unprimed HC trials). Fig. 1 (top right) shows that the greater the neural priming effect (i.e., the more primed Hs decrease in relation to unprimed Hs), the greater behavioural priming, and this positive relationship seemed consistent across the different regions (see smaller scatter plots).

It is also noteworthy the similarity in terms of location of brain activation between the results shown in Fig. 1 (top left) and those reported by Taylor et al. (2013). They found large clusters in the left parietal and posterior cingulate cortices when R and K hits were contrasted in their experiment. In order to ascertain whether these two regions in particular would also be modulated by priming in our experiment, we created 5 mm spheres around the peak coordinate of the left parietal (−36, −69, 36) and posterior cingulate (−9, −69, 33) cortices identified in the Taylor et al. study, and extracted the mean parameter estimates from the Hs-Ms contrast. Neural and behavioural priming were highly correlated in both regions (left parietal cortex: $r = .47$, $p < .05$; left posterior cingulate cortex: $r = .48$, $p < .05$ see Fig. 1, bottom).

Surprisingly, we did not observe activation in the hippocampus that survived our cluster correction for the Hs-Ms contrast. Considering the plethora of studies linking the hippocampus to successful recognition memory, particularly recollection memory (e.g., Daselaar, Fleck, & Cabeza, 2006; Diana, Yonelinas, & Ranganath, 2007; Gomes, Figueiredo, & Mayes, 2015; Mayes et al., 2007; Montaldi & Mayes, 2010), we decided to conduct a SVC analysis within the hippocampal volume using a probabilistic atlas of the bilateral hippocampus. Increased activity for Hs relative to Ms was found in the bilateral hippocampus (see Fig. 2, top left). Correlational analysis using the contrast primed minus unprimed HC Hs indicated a positive correlation between behavioural priming and neural priming in the hippocampus (Fig. 2, top right). Planned comparisons also revealed a significant difference between primed and unprimed trials for the Hs-Ms contrast, $t(16) = 1.90$, $p < .05$, $d = .46$ (see Fig. 2, bottom).

Next, we examined the masked priming effect by contrasting all primed trials against all unprimed trials, regardless of response category or confidence level. This contrast was conducted in order to ascertain whether different kinds of neural activity would subserve the RC versus BC experiments

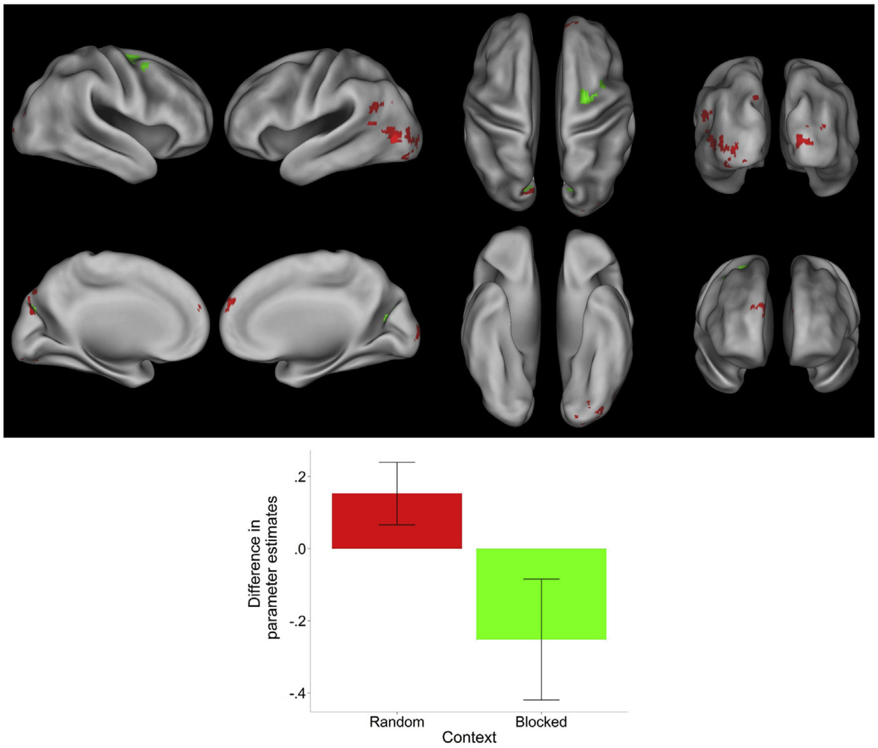

Fig. 3 – Top: Rendering of regions showing increased activity for primed relative to unprimed during the Random context experiment (red) as well as decreased in activity for primed relative to unprimed in the Blocked context experiment (green). Bottom: Average parameter estimates for the Random and Blocked context experiments within the regions detected in the Blocked and Random context experiments, respectively.

(see below the results for the BC experiment). If true, it would suggest that the same fluency cues derived from masked primes were interpreted differently by the brain depending on the type of context (Leynes & Zish, 2012). As can be seen in Fig. 3 and Table 3, extensive regions in the occipitoparietal network, most notably in the left parietal cortex and bilateral inferior/middle occipital gyrus, which extended into the left posterior MTG, exhibited increased activity for primed relative to unprimed words. Such pattern of neural activity for the RC experiment is consistent with that observed by Schnyer, Ryan, Trouard, and Forster (2002), who also employed a masked priming paradigm. Interestingly, in Schnyer et al.'s (2002) study, participants were only required to make word/non-word decisions on the target words (i.e., there was no recognition memory test). Thus, the fact that our study shows a similar neural activity pattern suggests that the increased

Table 3 – Brain regions exhibiting increased activation for primed versus unprimed words in the Random context experiment (top) and decreased activation for primed versus unprimed words in the Blocked context experiment (bottom). Approximate Brodmann areas (BA) are given in parentheses. L = Left, R = Right.

Region	Voxels	MNI coordinates			Z-scores
		x	y	z	
Random					
L middle occipital/temporal gyrus (BA 19,39)	290	−30	−82	−11	4.75
L parietal cortex (BA 7)	41	−24	−46	49	4.53
L cerebellum	34	−15	−64	−26	4.13
R medial superior frontal gyrus (BA 10)	42	9	62	28	3.87
L lingual gyrus (BA 17,18)	29	−15	−94	−8	3.87
R middle occipital gyrus (BA 18,19)	74	18	−94	10	3.86
L cuneus (BA 19)	36	−3	−82	28	3.56
Blocked					
R middle frontal gyrus (BA 6)	148	21	−4	49	4.52
R cuneus (BA 18)	37	24	−67	16	4.19
L superior occipital gyrus (BA 18)	27	−15	−79	25	4.15
L middle temporal gyrus (BA)	33	−30	−67	10	4.10
L putamen	30	−18	14	1	4.03
R putamen	33	21	17	−2	3.69

activity observed in these regions may be a possible neural marker of masked priming, rather than activity related to other mnemonic processes. The opposite contrast (unprimed > primed) did not reveal any significant clusters.

The observation that priming increased activity in the MTG in the priming contrast was interesting since this region was also found to be activated in our recognition memory contrast. This could indicate that the MTG may be acting as the integrative hub between fluency and recognition memory signals. Since we did not find an overlap between the priming and recognition memory MTG clusters we decided to ascertain whether the MTG region identified in the priming contrast would nevertheless also be sensitive to recognition memory. First, we determined all possible activation peaks in the priming contrast and selected the peak coordinate that was closest to the peak coordinate of the MTG identified in the recognition contrast. Next, we extracted the parameter estimates within a 5 mm sphere around the selected peak. Hs showed increased activity relative to Ms, $t(20) = 1.85$, $p < .05$, $d = .41$, indicating that a similar MTG cluster was indeed sensitive to both priming and recognition memory.

Note that although increased activity in some of the clusters identified in the primed versus unprimed contrast were also associated with recognition memory in the whole-brain contrast (e.g., left MTG, left parietal cortex) we do not believe that this was due to either participants really recognising the words or to conscious awareness of the primes. It is unlikely to be the result of correct recognition memory because similar results were obtained when restricting the analysis to FAs (i.e., primed FAs *vs* unprimed FAs), which consisted of unstudied words. It is also unlikely to be the result of some form of conscious awareness of the primes because both subjective and objective measures of awareness revealed that participants were completely oblivious that prime words had been presented between masks, so any influence of the masked primes must have necessarily been unconscious.

Finally, we wondered whether we would find greater functional coupling between the left MTG and other recognition-memory-related brain areas in the primed relative to the unprimed condition. If true, it could be indicative that this region may be assisting, through priming, in accessing memory information stored in higher-level brain regions. Given Taylor's et al. finding of the involvement of the left parietal and posterior cingulate cortex in masked priming, we decided to restrict our PPI analysis to these two particular regions. We created two ROIs of 20 mm spheres each, around the peak coordinate of the left parietal and posterior cingulate cortices identified in the whole-brain recognition contrast (10-voxel cluster extent, corrected for multiple comparisons). The left MTG showed increased connectivity with the left posterior cingulate cortex (BA 31, −27 −34 46, 15 voxels), and with the left parietal cortex (BA 39, −24 −61 43, 11 voxels) extending into the precentral gyrus (BA 4, −27 −19 40, 10 voxels), that was greater for primed relative to unprimed trials (see Fig. 4).

4.1.8. *Experiment 2 (BC experiment)*

Similar to the RC experiment, we conducted a whole-brain analysis using category (Hs, Ms, FAs, CRs) and prime status (primed, unprimed) collapsed across confidence level, and searched for voxels showing greater activity for Hs relative to Ms. Fig. 1 shows the results of this contrast, which, much like the RC experiment, revealed increased activity for Hs relative

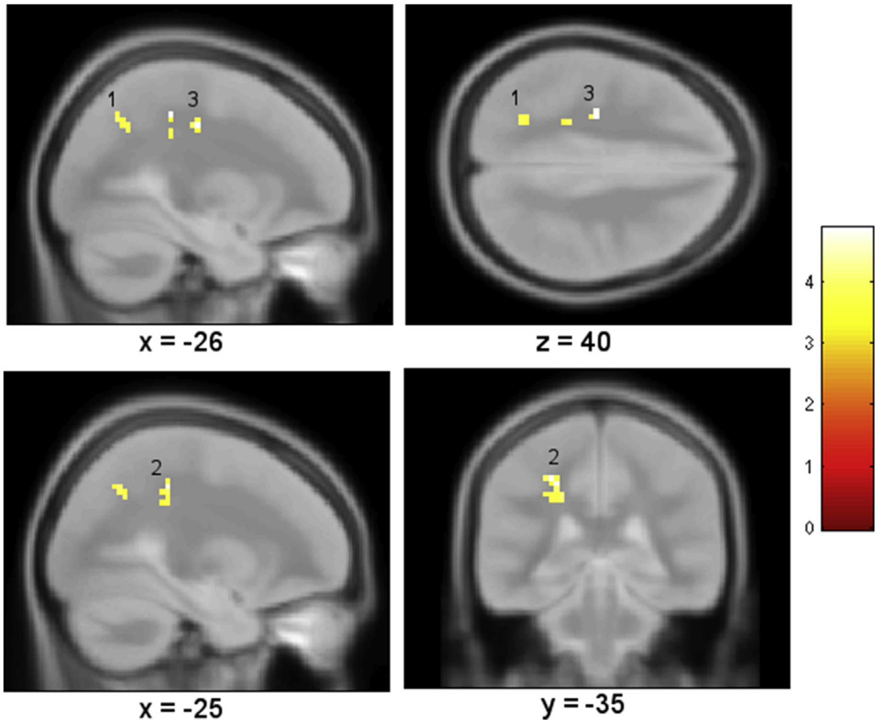

Fig. 4 – Surface rendering of brain regions showing increased connectivity with the left MTG (seed region) during the Random context experiment which was greater for primed versus unprimed trials. 1 = left parietal cortex, 2 = left posterior cingulate gyrus, 3 = left precentral gyrus.

to Ms in the left inferior parietal, posterior cingulate and left precentral cortices, brain regions commonly associated with successful recognition memory (Rugg & Vilberg, 2013). Interestingly, left MTG activation was absent in the BC experiment, even when a very lenient threshold was applied ($p < .05$, uncorrected). There was also no evidence of any brain-behavioural correlation in either the recognition memory regions identified in the Hs-Ms contrast (all $ps > .10$; see Fig. 1, top right), or the Taylor et al.'s regions (left parietal cortex: $r = -.10$, $p > .10$; left posterior cingulate cortex: $r = -.33$, $p > .10$; see Fig. 1, bottom).

For the SVC analysis of the hippocampus, we first determined which voxels were more active for Hs relative to Ms within the hippocampal cluster identified in the RC experiment (Fig. 2, top left, yellow area). Next, we extracted the parameter estimates from the Hs-Ms analysis and contrasted primed versus unprimed trials (see Fig. 2, bottom). There was no significant difference between primed and unprimed trials in the hippocampus, $t(19) = -.81$, $p > .10$, $d = .18$, and, critically, no significant correlations with behaviour were observed ($p > .10$; see Fig. 2, top right). This finding indicates that, contrary to the RC experiment, the hippocampus does not appear to have been affected by the priming manipulation, as indicated by the lack of correlation between our measures of neural (unprimed minus primed) and behavioural (primed minus unprimed) priming, thus, mirroring the behavioural data.

Regarding the masked priming effects, no voxel survived correction for the primed > unprimed contrast. However, when the contrast was reversed (i.e., primed < unprimed), large clusters in the right middle frontal gyrus, bilateral putamen, bilateral cuneus/middle occipital gyrus were significant (see Fig. 3 and Table 3). This result was interesting because it suggests that a simple manipulation of fluency context (RC *vs* BC) leads to the recruitment of completely different brain mechanisms, as reflected not only by distinct neural circuitry but also by a possibly different mode of retrieval (as indicated by increased activity for primed relative to unprimed in the RC experiment but the opposite in the BC experiment). Interestingly, even when the neural activity related to priming in one context was examined in the regions of the other context, a similar neural activation pattern was observed (i.e., "positive" priming [primed > unprimed] in the RC experiment for the BC regions; and "negative" priming [primed < unprimed] in the BC experiment for the RC regions, $t(29.99) = 2.15$, $p < .05$, $d = .66$, see Fig. 3, bottom).

4.1.9. *Interexperimental analyses*

We also directly compared recognition-memory-related activity between the RC and BC experiments by conducting a two-sample test using the images of the Hs-Ms contrast conducted at first-level. The only region that showed greater activation for the RC relative to the BC experiment was the right middle frontal gyrus (33, 41, 7; 52 voxels). The opposite contrast (i.e., BC > RC) did not reveal any significant clusters.

Next, we decided to run a conjunction analysis in order to determine how similar the pattern of brain activation was across the RC and BC experiments. Fig. 1 (top left; yellow areas) indicates the results from this analysis, which revealed an overlap in the precuneus, precentral gyrus, posterior cingulate and left parietal cortices. We then checked whether these four recognition regions would be sensitive to priming for Hs depending on the type of context by conducting a 2 Context (RC, BC) × 2 Prime Status (primed Hs, unprimed Hs) × 4 Region mixed repeated-measures ANOVA. There was an interaction between context and region, $F(2.34, 93.56) = 4.43$, $p = .01$, $\eta^2_p = .10$, as well as a trend for a context by prime status interaction, $F(1, 40) = 3.70$, $p = .06$, $\eta^2_p = .09$, which resulted from a positive difference between primed and unprimed Hs for the RC (primed Hs minus unprimed Hs = .19), whereas a negative difference was found for the BC (primed Hs minus unprimed Hs = −.36). The three-way interaction was not significant, $F(2.37, 95.55) = 1.83$, $p > .10$, $\eta^2_p = .04$.

Regarding the brain-behaviour correlations, the difference in the correlation coefficients between RC and BC experiments was significant in the left parietal and posterior cingulate cortices (both $ps < .05$), whereas the difference in the hippocampus approached significance, $p = .07$. For the SVC analysis of the hippocampus (Hs-Ms contrast), a 2 Context (RC, BC) × 2 Prime Status (primed, unprimed) mixed repeated-measures ANOVA revealed a trend for an interaction, $F(1, 40) = 3.54$, $p = .07$, $\eta^2_p = .09$, as the result of a positive primed-minus-unprimed difference in the RC, but a negative primed-minus-unprimed difference in the BC (see Fig. 2).

Finally, we computed a two-sample test for the priming contrast (primed > unprimed). For the RC > BC contrast, we observed increased activity in the bilateral cuneus/precuneus (left: −15, −82, 25; 44 voxels, right: 15, −76, 25; 48 voxels), right middle frontal gyrus (24, 14, 49; 165 voxels), right postcentral gyrus (45, −22, 46; 41 voxels) and the left MTG (−54, −55, 13; 74 voxels). The opposite contrast (i.e., BC > RC) did not reveal any significant clusters.

4.1.10. *Summary of the imaging data*

The imaging data can be summarised as follows: First, for both the RC and BC experiments, we observed higher activity in several regions previously associated with successful recognition memory (e.g., left parietal cortex, posterior cingulate cortex, hippocampus). However, only in the RC experiment did neural priming positively correlate with the size of behavioural priming during HC trials. The left MTG was also uniquely activated in the RC experiment and showed a functional coupling with the left parietal, posterior cingulate and precentral cortices that was greater for primed versus unprimed trials. Second, masked priming was characterised by a completely different pattern of neural activity between RC (primed > unprimed trials in several occipitotemporal and frontal regions) and BC (primed < unprimed trials in the middle frontal gyrus, precuneus and insula) experiments.

5. Discussion

The present fMRI study aimed at investigating whether recognition memory accuracy could be influenced by means of a masked repetition priming manipulation with LF words (RC experiment, Experiment 1). The second major aim was to determine how fluency context impacted neural activity by running the same paradigm of Experiment 1, but grouping primed and unprimed trials in two separate blocks (BC experiment, Experiment 2). As a third aim, we explored the differences in the neural correlates of masked repetition priming between the two types of context. The behavioural data indicated that for the RC experiment (i.e., primed and unprimed words randomly intermixed), priming selectively enhanced recognition memory accuracy for HC, but not LC, trials. This increase in recognition accuracy due to priming was also accompanied by activity changes in several recognition-memory-related regions (e.g., left parietal cortex, left precentral gyrus, left MTG, posterior cingulate cortex and bilateral hippocampus). Neural priming in the left parietal and posterior cingulate cortices positively correlated with the size of behavioural priming during HC trials and showed increased connectivity with the left MTG for primed versus unprimed trials. Regarding the BC experiment (i.e., primed and unprimed words presented in separate blocks), although participants seemed to rely on many of the same brain regions used during recognition memory in the RC experiment, the left MTG was not recruited in the BC experiment. In addition, for the BC experiment, there were no correlations between neural and behavioural priming in any recognition memory regions. Finally, there were distinct patterns of neural activity for masked priming depending on the type of fluency context. Increased activity was observed in several occipitotemporo-frontal regions in the RC experiment, whereas decreased activity was observed in right middle frontal gyrus, putamen and extrastriate cortex in the BC experiment.

5.1. *Priming only affected recognition memory when fluency context was random*

One of the critical and most interesting findings of the present study was the observation that, in the RC experiment, recognition memory accuracy for primed words was increased relative to unprimed ones. Such increase in recognition accuracy due to a fluency manipulation is consistent with Leynes and Zish's study, which indicated that more fluent items were associated with greater accuracy than less fluent ones, and that this effect was correlated with the FN400, an ERP component commonly linked to familiarity (e.g., Bridger, Bader, Kriukova, Unger, & Mecklinger, 2012; Nessler, Mecklinger, & Penney, 2005; Rugg & Curran, 2007; Voss, Lucas, & Paller, 2012). Our results showed that the effect priming had on recognition memory was restricted to HC trials; recognition was at chance for the LC condition and there was no evidence that priming influenced recognition accuracy for LC trials.

Although slightly tangential to our research questions, it is not clear whether the HC condition in our experiment reflects either strong familiarity, recollection, or both. Although it is likely that the HC condition contains memories that are based on both familiarity and recollection, one possibility is that our masked priming manipulation increased the incidence of recollection to a greater extent than familiarity. Taylor and Henson (2012) observed an increase in recollection following priming that occurred for Hs but not for FAs, which led the authors to suggest that priming increased retrieval of internal source. In contrast, fluency-driven familiarity was indicated by a similar impact of repeated primes on both Hs and FAs for words judged to be familiar. In the present study, Hs were more greatly affected by priming than FAs in the HC condition, whereas priming affected Hs and FAs similarly in the LC condition (see Table 1). Given this pattern of results and their correspondence with Taylor and Henson's findings, it is tempting to conclude that recollection occurred more frequently than familiarity during HC trials, whereas the opposite was true during LC trials.[3] Our fMRI results also indicated that successful recognition memory recruited many brain structures believed to support recollection, including the left parietal cortex and posterior cingulate cortex (whole-brain analysis), as well as the bilateral hippocampus (SVC analysis).

If participants did recollect a significant portion of the words in the HC condition, then our study would suggest that enhanced fluency may also increase objective recollection memory, and not only familiarity memory as Leynes and colleagues observed (Bruett & Leynes, 2015; Leynes & Zish, 2012). Nevertheless, as we indicated above, we acknowledge that not being able to confidently argue in favour of either familiarity or recollection is a limitation of our study. It is possible that our behavioural and imaging data reflect a combination of very highly-confident familiarity and recollection memory. Thus, future research will be required to determine whether our effects apply to both familiarity and recollection, or whether they are specific to only one type of memory.

5.2. *Blocking prime status prevented priming from increasing recognition memory judgements*

Interestingly, the BC experiment appeared to entail a similar kind of conscious memory experience as the RC experiment (a conjunction analysis revealed a large overlap in several recognition-memory-related brain structures; see Fig. 1, top left). Critically, however, we found no significant brain-behaviour correlations between neural and behavioural priming in either the posterior cingulate cortex, left parietal cortex or hippocampus for the BC. We do not believe absence of these effects are due to a Type II error for two reasons. First, the two experiments were matched in all respects (stimuli used, number of trials, number of participants, statistics conducted, etc.) except fluency context. It is therefore unlikely that in one case (RC experiment) medium-to-strong correlations are detected, whereas in the other (BC experiment) there is no evidence whatsoever for a similar but weaker effect (in fact, in some situations, even the opposite trend is observed, see Fig. 2). Second, the correlational analysis closely mirrored what occurred behaviourally. Specifically, there was no influence of priming on recognition responses during HC trials in the BC experiment, so one would not have expected priming to have influenced brain activity during recognition memory.

Thus, the fact that priming was ineffective at enhancing recognition memory during the BC experiment is strong evidence that the increase in recognition memory through

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[3] It should be noted, however, that recollection was not affected by the masked priming manipulation when repeated primes were used in Taylor and Henson's study (the influence of priming on claims of recollection was only shown for conceptual primes).

priming is only effective when fluency varies from trial-to-trial as in the RC experiment. One possibility could be that, in the RC experiment, repetition fluency (fluency derived from the study phase [old *vs* new words]) interacted with perceptual fluency (fluency derived from the masked priming manipulation [primed *vs* unprimed words]), resulting in an amplified fluency signal for Hs, which is consistent with Leynes and Zish's view of a dynamic interaction among different fluency cues. This signal amplification may have, in turn, enhanced the probability that the entire memory trace for the studied words was retrieved, and, thus, successful memory occurred (Taylor & Henson, 2012; Taylor et al., 2013).

5.3. *The MTG as an integration site for binding multiple sources of memory information*

As mentioned above for the RC experiment, the greater the effect priming had on recognition accuracy, the greater the reduction of the BOLD response in recognition-memory regions for primed relative to unprimed words. This positive correlation seems consistent with findings within the priming literature, in which the greater the reduction in neural activity for primed relative to unprimed items, the larger the size of behavioural priming in priming-sensitive brain regions. Such findings may relate to the tuning of memory representations of the repeated items and/or access to automatic stimulus-response links (e.g., Henson, Eckstein, Waszak, Frings, & Horner, 2014; Horner & Henson, 2008; Schacter, Dobbins, & Schnyer, 2004; Wiggs & Martin, 1998). Furthermore, a recent study (Gomes, Figueiredo, & Mayes, 2016) reported reductions in activity for primed relative to unprimed object associations in the hippocampus, suggesting that neural priming is not limited to cortical structures involved in the retrieval of perceptual and/or conceptual information. Also, Gagnepain et al. (2011) found that priming produced decreased, not increased, encoding-related activity in the medial temporal lobe for words that were subsequently recollected. This contrasted with the increased activity for unprimed stimuli in the same region for later recollected words. Based on their connectivity analysis, Gagnepain et al. concluded that repetition suppression in the left superior temporal gyrus may have been transmitted to the medial temporal lobe for stimuli that were later recollected, generating the activity reductions in that area.

It is interesting to note that a left MTG cluster (which was close to the ventral part of the superior temporal gyrus in Gagnepain et al.'s study) was uniquely activated during recognition memory in the RC experiment. Furthermore, the PPI analysis revealed that this left MTG region was more functionally connected to the left parietal and posterior cingulate cortex during primed relative to unprimed trials (see Fig. 4). These two brain structures are involved in the storage of memory information (e.g., Vilberg & Rugg, 2007b, 2009), and, in the present study, neural priming in these regions (primed HC Hs < unprimed HC Hs) correlated strongly with behavioural priming. Given this data pattern, we propose that the greater behavioural performance associated with reduced activity for primed relative to unprimed Hs in recognition memory regions (e.g., left parietal cortex, posterior cingulate cortex) may be due to the direct influence of the left MTG in those regions. This modulation possibly only takes place when the masked primes act as efficient retrieval cues, as may well be the case in the RC experiment, leading to, for instance, advanced neural activity (e.g., Gagnepain et al., 2008; Henson, 2003; James & Gauthier, 2006) or a decrease in the prediction error (e.g., Friston, 2005, 2008) for recognised and primed stimuli. In other words, sensory evidence accumulating in the left MTG could guide a more efficient retrieval of memory information, making this information more readily accessible and, consequently, leading to a reduced neural response for primed relative to unprimed HC Hs.

Although speculative, the idea that the left MTG may behave as an integration site is not new (see Lau et al., 2008, for a review). Some researchers have already advocated that lexical-semantic and multimodal integration may be one of the core functions of the MTG/superior temporal sulcus (e.g., Amedi, Von Kriegstein, Van Atteveldt, Beauchamp, & Naumer, 2005; Beauchamp, 2005a, 2005b; Turken & Dronkers, 2011).

Together, our data point to the possibility that the left MTG may integrate different fluency signals that are used to guide a more efficient retrieval of mnemonic information in recognition memory structures, reducing neural activity for primed relative to unprimed words in those recognition regions. Future research will be needed to confirm whether or not our interpretation is correct.

5.4. *Masked priming recruited distinct neural networks for RC and BC experiments*

The observation of a completely distinct pattern of priming-related activation changes between the RC and BC experiments is noteworthy. In the RC experiment, when primed and unprimed trials were randomly intermixed, large clusters in the occipitotemporal cortex (including the fusiform gyrus, middle occipital gyrus and left MTG), as well as in the left parietal cortex and superior frontal gyrus, were shown to increase in activity for primed relative to unprimed words. In contrast, when primed and unprimed words were presented in separate blocks, not only was a different group of brain structures recruited (right middle frontal gyrus, precuneus, putamen) but also the direction of the BOLD response was opposite to that observed in the RC experiment (i.e., reduced activity for primed *vs* unprimed words). It should be noted that every experimental variable other than the fluency context (i.e., RC *vs* BC) remained constant between the two kinds of experiment (same word stimuli, same scanner, same instructions, same procedure, same statistical analysis, etc.). Since both experiments yielded similar results in the Hs-Ms whole-brain contrast (e.g., see Fig. 2), it suggests that differential neural activity was specific to the fluency context and not to an unknown factor that could yield systematic differences in the neural response between the two experiments.

To our knowledge, only one study showed a similar difference in neural activity between two different masked priming tasks (Nakamura, Dehaene, Jobert, Le Bihan, & Kouider, 2007). In this study, a reading task led to repetition enhancement in the left ventral premotor cortex, left fusiform gyrus and left inferior parietal cortex, of which the latter two were also activated for primed words in the RC experiment of the present study. In contrast, a semantic categorisation task led to repetition suppression in the left middle temporal gyrus, as we also observed in our BC experiment. Despite the tantalising similarities between Nakamura et al.'s results and ours, we should note that the reading and categorisation tasks naturally required different instructions, which led the authors to conclude that “the task instructions engaged by participants induce a biasing influence over the task-relevant regions even for unconsciously perceived stimuli” (Nakamura et al., 2007, p. 19646). Because we used the exact same procedure (and associated instructions) for the RC and BC experiments, such biasing would not be expected to account for the different pattern of neural data between the two experiments.

Another study has also observed repetition suppression and enhancement when familiar and unfamiliar stimuli were repeated, respectively, even though the task was the same for both types of stimuli (Henson, Shallice, & Dolan, 2000). The authors proposed that repetition suppression for familiar stimuli reflects more efficient processing, whereas repetition enhancement for unfamiliar stimuli reflects the engagement of additional physiological processes, such as the formation of new representations. In the present study however, the exact same (unfamiliar) words were used in both experiments, so it is not clear why they would recruit different regions and be sensitive to different contrasts (i.e., primed > unprimed for RC, and primed < unprimed for BC).

Since our fMRI study is the first, to the best of our knowledge, to directly compare priming-related activation changes between RC and BC primed trials in the masked priming paradigm, we can only speculate about the reasons for such a striking divergence. One possibility could be that participants were unconsciously evaluating the significance of the masked prime cues, and further determined their use as the experiment progressed. Thus, when prime status varied randomly, the masked primes of primed words may have functioned as useful cues for initiating a search process that would be advantageous for making recognition decisions. It could be that the system allocates increased attention in the interest of this search process, which might explain why priming was characterised by activations (i.e., primed > unprimed) as opposed to deactivations (i.e., primed < unprimed) in the RC experiment. Indeed, Nakamura et al. (2007) argued that repetition enhancement in their study for the reading-aloud condition may have occurred because reading requires central attention.

In contrast, for the BC experiment, the unchanging nature of the fluency context prevented variations in fluency that would, otherwise, have made these words useful as recognition cues (Leynes & Zish, 2012). Because the repetition of items during a priming test phase often leads to decreased activity for the repeated items (e.g., Henson, 2003; Schacter et al., 2004), the reduced activation for primed versus unprimed trials in the BC experiment may have reflected a typical repetition suppression effect that related to facilitated word processing. This idea gains support when we consider that the regions involved in the priming effect for the BC experiment (e.g., left MTG, right medial frontal gyrus) have also exhibited repetition suppression in word repetition (e.g., Lin & Ryan, 2007; McDonald et al., 2010) and semantic (e.g., Giesbrecht, Camblin, & Swaab, 2004; Rissman, Eliassen, & Blumstein, 2003) priming studies. Moreover, we also observed reduced activity in the bilateral putamen, a region that is often reported in linguistic and semantic neuroimaging studies (e.g., Klein, Zatorre, Milner, Meyer, & Evans, 1994; Price, Moore, Humphreys, & Wise, 1997) and has also been implicated in semantic matching during priming (e.g., Rossell, Bullmore, Williams, & David, 2001). Thus, our neural masked priming effect in the BC experiment may have reflected facilitation in the access to, or retrieval of, perceptual, phonological and/or semantic information encoded during the study phase.

5.5. *Limitations of the present study*

One potential limitation of our study is that our interpretations were mostly based on the results obtained in the separate analysis of the RC and BC experiments. The inter-experimental analyses revealed some trends, but overall most effects were unreliable. It is possible however, that these weak effects are the consequence of having fluency context as a between-subject factor – the difference between the small but meaningful masked priming effect between RC and the BC experiments may have been masked by large between-subjects variance. Our decision to include fluency context as a between-subject variable was because we wished to make our context manipulation as similar as possible to that of Leynes and Zish (2012) and Westerman (2008) who also used fluency context as a between-subject factor and performed separate analysis for each experiment. To increase statistical sensitivity, future studies could manipulate fluency context within-subjects; for instance, the same participants could perform the RC and BC experiments on different sessions (the order counterbalanced across participants). This procedure may be statistically more powerful in detecting direct differences between the two experiments.

Another critical point that could be raised is the relatively low number of trials in each confidence level, which prevented using the same design matrix across all participants. To forestall this issue, future studies could include only two confidence choices (low *vs* high), as opposed to four as in the present study, and perhaps increase the number of stimuli.

6. Conclusion

Priming studies rarely take into account the (intentional or unintentional) presence of context effects. Our simple manipulation of blocking prime status eliminated the effect priming had on recognition memory performance. It is thus possible that even subtler changes in fluency context may still have an effect on individuals' decisions. Given that visual masked priming is widely used as a tool to investigate a variety of visual phenomena, it is important that future research explores the extent to which context effects become non-trivial and how they influence test decisions that are not limited to recognition judgements (e.g., likability judgements). It will also be critical to understand whether the same priming-sensitive recognition memory regions detected in the present study also subserve other forms of neural priming, such as priming for novel associations (Dew & Giovanello, 2010; Gomes et al., 2016; Gomes & Mayes, 2015b) and S-R learning (e.g., Gomes & Mayes, 2015a; Horner & Henson, 2008, 2011, 2012). Finally, recent research indicates that pupillary responses can discriminate between studied but completely forgotten items and unstudied items (Gomes, Montaldi, & Mayes, 2015b). It will be interesting to combine the current paradigm with pupillometry to determine whether the pupil will also be sensitive to fluency context.

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