

The effect of negative arousal on declarative memory

Marianna Constantinou^{a,1,*}, Katherine Karadachka^{b,1}, Lars Marstaller^c, Hana Burianová^d

^a Department of Psychology, Bournemouth University, UK

^b Radboud University Nijmegen, Donders Institute for Brain, Cognition and Behaviour, Donders Centre for Cognitive Neuroimaging, Nijmegen, the Netherlands

^c Porsche Engineering, Prague, Czech Republic

^d Department of Psychology, Swansea University, Swansea, UK

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ABSTRACT

Arousing events influence retrieval success, with a number of studies supporting a context-dependent effect of arousal on episodic memory retrieval. An improvement in speed and accuracy of episodic memories is observed when negative arousal is attached to them. In contrast, enhancing effects of negative arousal have not been reported to improve semantic memory retrieval. Episodic and semantic memory are highly interactive and yet differ based on their embedded contextual content. Although differences in brain activity exist between episodic and semantic memory, the two types of memory retrieval are part of a common long-term memory system. Considering the shared processes between episodic and semantic memory, the objectives of the current study were twofold: i) to examine, employing a novel paradigm, whether performance on episodic and semantic memory retrieval would be influenced differently by varying levels of arousal, between negative and neutral valence; and ii) to explore the neural patterns underlying these processes. Forty-seven healthy young adults were recruited and completed the experiment in the MRI scanner. The results demonstrated a negative arousal effect on the brain circuitry subserving both memory conditions as well as on behavioural performance, as indicated by better accuracy and faster reaction times. The study provides an insight into the role of negative arousal in memory processes and contributes to our understanding of the interplay between cognitive and emotional factors in memory modulation. Our work also highlights the highly interactive nature of episodic and semantic memory, and emphasises the importance in understanding how negative arousal interacts with the contextual content of a memory, on a behavioural and neurofunctional level.

1. Introduction

Emotional stimuli influence declarative memory retrieval by evoking a state of arousal, which can be represented as a physiological level of arousal (high or low) or as a perception of valence of the stimuli (positive or negative; Alger et al., 2018). Biologically, a prolonged retention of negative arousing information in memory serves evolutionary purposes, facilitating future decisions (Gershman and Daw, 2017; Payne and Kensinger, 2018) and survival by prioritising actions that enable the mitigation of potential threats (Hartikainen, 2021). Such observations might account for findings showing that negative stimuli, in contrast to positive ones, are linked to heightened vividness during retrieval (Mickley and Kensinger, 2008). On a neural level, the beneficial effects of negative arousal work by modulating competing representations and enhancing elaboration and long-term consolidation (Ponzio and Mather,

2014). Behaviourally, these effects seem to be sustained throughout the adult lifespan (Kensinger and Schacter, 2005; Nashiro and Mather, 2011). The effect of arousal on memory retrieval has been found to be context-dependent. For example, episodic declarative memories (and episodic-laboratory memories), conceptualised as recollections of experiences and objects containing a lot of contextual information (LaBar and Cabeza, 2006), are retrieved more accurately if related to high arousing stimuli (for review see Dolcos et al., 2017; Kensinger et al., 2007). Although the context-dependent effect encompasses both negative and positive stimuli, our current work specifically focuses on the role of negative arousal on memory processes. While enhancing effects of negative arousal have been reported for episodic memory, this influence has not been found to improve semantic declarative memory retrieval (Dew et al., 2014; Hall et al., 2020), related to factual information and general knowledge and containing the least amount of

* Corresponding author. Department of Psychology, Bournemouth University, Fern Barrow, Poole, BH12 5BB, UK.

E-mail address: mconstantinou@bournemouth.ac.uk (M. Constantinou).

¹ KK & MC share first authorship.

contextual details (Tulving, 1972). To our knowledge, no study thus far has examined the arousal effect on episodic-laboratory and semantic memory retrieval together, and thus the functional underpinnings of these processes remain unclear. This is important since episodic and semantic memory engage shared processes of a common long-term memory (LTM) network (Burianová and Grady, 2007; Burianová et al., 2010). Significantly, deficits in declarative memory, which can manifest as both decreased and increased retrieval performance, are present in a multitude of disorders, such as schizophrenia (Olsen et al., 2015), major depressive disorder (Dere et al., 2010), and post-traumatic stress disorder (Lambert and McLaughlin, 2019; Brown et al., 2014). Understanding how arousal interacts with the contextual content of memories is important, considering the alterations in memory performance in these disorders, based on the arousal level of studied material, as well as the associated changes in arousal patterns across these disorders.

Evidence has shown that arousing, compared to non-arousing items, are retrieved more accurately at immediate recall and at a later time (Sharot et al., 2004; Adolphs et al., 2005; Sharot et al., 2007; Nielson and Powless, 2007; Sharot and Yonelinas, 2008; Ritchey et al., 2008; Liu et al., 2008; Ritchey et al., 2011; Schumann et al., 2018). Furthermore, beneficial retrieval effects from exposure to arousing stimuli carry over to neutral items encountered prior to, and a week after exposure (Anderson et al., 2006; Tambini et al., 2017). One explanation comes from the arousal-biased competition model, which states that arousal biases processing resources toward high priority information at a cost of low priority representations (Mather and Sutherland, 2011). On a neural level, Andreano et al. (2017) showed that stronger connectivity within the salience network was related to a more accurate retrieval of neutral material learned under negatively arousing conditions. Further evidence from functional neuroimaging studies has implicated bottom-up and top-down mechanisms for emotional enhancement of memory, namely a direct medial temporal lobe (MTL)-based circuit involved in bottom-up neurohormonal interactions during encoding, consolidation, and retrieval, as well as an indirect non-MTL based mechanism involving prefrontal and parietal areas underlying executive and semantic processes, which can be influenced by valence (for review Dolcos et al., 2017). Co-activation of amygdala and hippocampus has been identified as a key component for processing of emotional memory (Dolcos et al., 2005), where the amygdala engages during encoding (Sergerie et al., 2006), consolidation (Ritchey et al., 2008), and retrieval (Dolcos et al., 2005; Kensinger and Schacter, 2005; Sergerie et al., 2006) of salient information, while the hippocampus binds the elements of the salient experience with a memory trace (Ranganath, 2010). According to Madan et al. (2012), processing of negative arousing stimuli enhances retrieval accuracy for individual items while simultaneously impairing associative binding between them. Some evidence indicates that arousal of negative valence down-modulates hippocampal activity, resulting in weakened associational processing and facilitating amygdala-based encoding of the individual arousing items (Bisby and Horner, 2018). More recently, Madan et al. (2017) found that hippocampal activity is not completely down-modulated, but instead the left hippocampus might provide a compensatory role in processing of negative arousing items. Specifically, following the presentation of negative arousing information, conventional encoding processes supported by MTL regions may be challenged. In response, the hippocampus might be taking on an additional role ensuring that the negative arousing items are still encoded effectively. While numerous studies have focused on episodic memory retrieval, there has been a notable lack of evidence regarding the role of arousal on semantic memory retrieval. This study is thus the first to directly compare the arousal effect on both episodic-laboratory and semantic memory retrieval, providing an examination of the influence of emotional arousal on distinct memory processes.

Our previous work shows that semantic and episodic memory are part of a common LTM system (Burianová and Grady, 2007; Burianová et al., 2010), although differences in brain activity and connectivity are

found for the two types of memory retrieval alongside the contextual continuum. We established a novel functional imaging paradigm, designed to measure behavioural and neural performance solely related to declarative memory retrieval. The task presents participants with a series of visual stimuli, followed by cues responsible for prompting either episodic-laboratory or semantic retrieval. Findings demonstrate that despite differing according to their contextual content, episodic-laboratory and semantic memory are subserved by a large-scale unitary memory network, with some unique activation patterns related to each of the memory types (Burianová and Grady, 2007; Burianová et al., 2010; for review Palacio and Cardenas, 2019). In the present study, we adapted this memory retrieval task and modified it by dividing the retrieval demands into four conditions: episodic-laboratory high arousal, episodic-laboratory low arousal, semantic high arousal, and semantic low arousal. The present study was designed to determine the effect of arousing stimuli on episodic-laboratory and semantic memory retrieval, which are highly interactive and yet retain some distinctiveness according to their embedded contextual content (Burianová and Grady, 2007; Burianová et al., 2010). While episodic memories are heavily linked to their unique temporospatial context, semantic memories are being retrieved without reliance on the original context in which they were formed (Renoult et al., 2019). In this investigation, we aimed to explore whether performance on these two memory types would be affected differently by the varying levels of arousal, specifically high negative arousal, compared to low neutral arousal, as reflected in response accuracy and reaction time. Using Partial Least Squares (PLS) analysis we further examine the neural patterns underlying these processes. PLS analysis is a multivariate statistical technique that examines the complex relationships between large-scale brain activity and experimental paradigm, such as the manipulation of arousal levels in our exploratory study. Given the shared processes between episodic and semantic memory, we expected to find a negative arousal effect on the brain circuitry subserving both memory conditions as well as on behavioural performance, as indicated by better accuracy and faster reaction times.

2. Methods

2.1. Participants

Forty seven right-handed healthy young adults (mean age = 24.25 years; SD = 3.45; 25 males) were recruited. Inclusion criteria involved normal or corrected-to-normal vision, absence of neuropsychiatric disorders or head trauma, a history absent of medications affecting cardiovascular responses (e.g., antidepressants) and a minimum education level of a higher education diploma to encourage homogenous semantic knowledge. To meet MRI compatibility, participants did not have metal implants in their body.

Prior to conductance of the study, approval was attained from the Ethics Committee of the Psychology Department of Swansea University. Information sheets were distributed to the participants and informed consent was provided upon study commencement.

2.2. Stimuli

2.2.1. Experimental stimuli

Thirty colour photographs, portraying either neutral or negative objects/scenes, were used as visual-arousing cues for the memory retrieval conditions. Stimuli were selected from the Open Affective Standardized Image Set (OASIS) database (Kurdi et al., 2017), based on their evoked arousal ratings. Fifteen photographs depicted highly negatively arousing events (e.g., photograph of an injured male) and fifteen depicted low arousing neutral events (e.g., photograph of a park), deviating by two standard deviations from the mean in each direction.

2.2.2. Control stimuli

Five black and white photographs were used as control stimuli. Stimuli used during the experimental trials were manipulated into scrambled images using a Matlab script. The purpose of the control condition was to remove memory retrieval processes from the trial, while still providing a visual (albeit meaningless) stimulus and a motor response.

2.3. Task

The task utilized an established paradigm (Burianová and Grady, 2007; Burianová et al., 2010) and adjusted it to account for arousal effects. The task comprised two memory retrieval conditions (episodic-laboratory memory retrieval and semantic memory retrieval), two arousing conditions (highly negatively arousing and low arousing), and a control condition. All trials started with the presentation of a highly negatively arousing or low arousing image. Each image was presented twice, in a non-sequential order, to ensure long-term memory engagement and to provide identical stimulus presentation across the two memory conditions. A statement, prompting either episodic-laboratory or semantic memory retrieval, followed, accompanied by three possible responses (i.e., 1 = “True”, 2 = “False” and 3 = “I don’t know”). Episodic-laboratory statements required the retrieval of a particular aspect of the previously presented image (e.g., “In the picture, the dog’s mouth is open” to an image of a dog attack). It is worth noting that the episodic-laboratory memory statements targeted the retrieval of a central detail of the image, regardless of arousal level, ensuring that the specific aspect of the image being retrieved was consistently tied to the arousal manipulation, minimising potential variations between high negative and low arousing conditions. Semantic retrieval statements were related to general-world knowledge about the content of the previously presented image (e.g., “Dogs are inherently savage” to an image of a dog attack). Each semantic statement was carefully designed to align with the arousal level of the corresponding image. This intentional matching allowed us to investigate the influence of arousal on semantic memory retrieval. Regarding the control condition, both the effect of arousal and the memory retrieval aspect were absent. Following the presentation of a scrambled image, an unrelated statement was introduced (e.g., “Press a key that corresponds to the letter V”), securing a

consistent perceptual experience across the conditions, whilst discarding the effect of arousal and memory retrieval. For a schematic representation of the task, please see Fig. 1.

2.4. Experimental procedure

For each experimental trial, a highly or low arousing image was presented for 4 s, followed by an inter-stimulus interval (a blank screen) for 1 s, then a memory-retrieval statement was presented for 6 s, followed by an inter-trial interval (fixation cross) for 1 s, which was jittered depending on response speed (i.e., the duration of the ITI depended on how quickly the participants responded to the statement presented within 6 s. The statement disappeared for responses earlier than 6 s and the remaining time was added to the duration of the fixation cross presentation). A mirror attached to the head coil enabled the visual observation of the task and behavioural responses were gathered via an MRI-compatible response box. Participants were instructed to use their right hand with their index finger on button 1 for “True”, middle finger on button 2 for “False”, and ring finger on button 3 for “I don’t know”. The scanning session included one 13-min functional run and a 5-min structural run. 60 experimental (30 episodic-laboratory statements, 30 semantic statements) and 10 control trials were presented in a counterbalanced order. Once the task was concluded, participants were debriefed on the purpose of the study.

2.5. Experimental design

The experimental design was a 2×2 within-subjects, with factors Memory (episodic/semantic) and Arousal (high/low). The dependent variables included brain activations, as measured by the BOLD effect (Ogawa et al., 1990) and, behaviourally, reaction times and accuracy.

2.6. Data acquisition & analysis

2.6.1. Data acquisition

Brain images were collected with a 3T Siemens Magnetom Verio scanner and a 32-channel head coil at Swansea University. A T1-weighted anatomical MRI was acquired using an MP2RAGE sequence with 176 sagittal slices, TR = 4000 ms, TE = 2.98 ms, FOV = 256 mm,

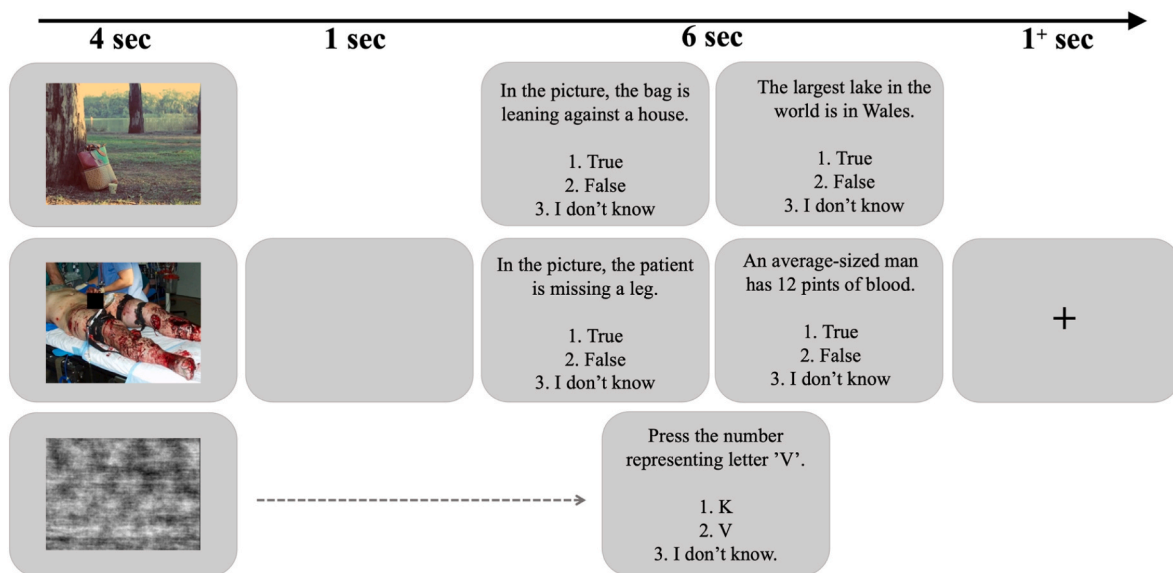


Fig. 1. Schematic representation of the task design. Each trial started with the appearance of an image (4 s). The picture acted as a a) high negative arousing cue; b) low arousing cue; c) control stimulus, abandoning effects of arousal. Following image presentation, a 1-sec inter-stimulus interval (ISI) was preceded by the statement (6 s). The statement involved a question eliciting i) episodic retrieval, ii) semantic retrieval or iii) no retrieval. This was followed by a jittered inter-trial interval (ITI) during which a fixation cross was displayed on the screen (1+ sec).

flip angle = 6°, and voxel size = 1 mm³. Functional images were collected with a T2*-weighted echo-planar image sequence (45 axial slices, TR = 3000 ms, TE = 30 ms, FOV = 190 mm, flip angle = 90°, voxel size = 2.5 mm³).

2.6.2. Data preprocessing

Image preprocessing was carried out utilizing Statistical Parametric Mapping (SPM12) (<https://www.fil.ion.ucl.ac.uk/spm/software/spm12/>) software. The following steps were applied to each dataset: realignment of functional images to correct for head motion, coregistration of functional and structural images, segmentation of the structural image with a forward application of deformation fields, normalization of the realigned images into a standardized space (in accordance with the Montreal Neurological Institute [MNI] template) with 4th Degree B-Spline Interpolation, to a voxel size of 2 × 2 × 2 mm, and smoothing of the normalized images with a 6 mm full-width-at-half-maximum 3D Gaussian kernel. No participants were excluded from the analyses due to excessive motion, as none of the participants exhibited head movement exceeding 2 mm.

2.6.3. Data analysis

Imaging data were analyzed by Partial Least Squares (PLS; [Mcintosh et al., 1996](#)) analysis, to examine brain activity alterations induced by task demands (Task PLS; *i.e.*, memory retrieval and state of arousal) and related to the behavioural variables (accuracy and reaction times). PLS is a multivariate analytical technique, which identifies patterns of covariance over each brain voxel and condition. Thus, this method utilizes the assumption that cognition engages a consolidated and spatially-distributed pattern of neural activations. Briefly, a single matrix is decomposed by singular value decomposition, generating a hierarchical arrangement of latent variables (LVs), which delineate both the common and unique patterns between brain activations and experimental design or behaviour. Contrary to univariate methods, contrasts are not defined; instead, interpretation relies on the accounted covariance of significant LVs. For each LV, PLS produces an image of voxel saliences (*i.e.*, indication of neural activity modification according to experimental condition or behaviour), a profile of task saliences (*i.e.*, the influence of brain activity over conditions), and a singular value (*i.e.*, the percentage of LV accounted covariance). As such, correcting for multiple comparisons is not necessary since all voxels and conditions are entered into a single analysis.

For the purposes of this study, two Task PLS analyses and one Behavioural PLS analysis were conducted on the event-related data obtained from accurate trials. All PLS analyses in this study were mean-centered, allowing for the examination of relative differences and commonalities in brain activity across conditions. The first Task PLS analysis aimed to identify a pattern in brain activity common to all memory conditions and a separate pattern of brain activity for the control condition. This analysis aimed to replicate our previous findings ([Burianová and Grady, 2007](#); [Burianová et al., 2010](#)). The second Task PLS analysis specifically focused on the experimental conditions and sought to delineate the difference in brain activity between memories cued by highly arousing negative stimuli and memories cued by non-arousing neutral stimuli, capturing the arousal effect. Lastly, the Behavioral PLS analysis aimed to investigate the relationship between the negative arousal effect on memory retrieval and performance measures such as accuracy and reaction times. As with the Task PLS analyses, the Behavioral PLS analysis also employed mean-centering to ensure a consistent analytical approach across all analyses.

Analyses were conducted on a 15-s period (temporal window of size 5 TRs), starting at the onset of statement presentation following the arousing cue. Activity at each time point was normalized to activity in the first TR of the statement period, to avoid any effects from upcoming trials. To acquire a summary measure of the spatial pattern of every condition across each LV, brain scores were calculated, indicating the salience of each voxel and BOLD signal. Saliences are represented in

positive or negative values, depending on the voxel's relation to the pattern of task-dependent differences identified by the LV.

Statistical significance of each LV was assessed with permutation testing, repeated 500 times. To further evaluate the reliability of activations identified by permutation testing, bootstrapping was used and repeated 100 times. This calculated the standard error across voxel salience for each LV. Voxels with a bootstrap ratio greater than 3.0 were accounted reliable, approximating $p < 0.001$. Confidence intervals of brain scores for each LV were then calculated at 95%.

3. Results

3.1. Behavioural results

Behavioural performance was assessed by comparing the means of accuracy and reaction times (correct trials only) across the four experimental conditions, using two 2 (Memory: episodic/semantic) × 2 (Arousal: high/low) repeated-measures Analyses of Variance (ANOVAs).

For accuracy, we report a significant trend of Memory, which approached significance, $F(1, 46) = 3.84, p = 0.056, \eta_p^2 = 0.077$, and a significant main effect of Arousal, $F(1, 46) = 30.81, p < 0.001, \eta_p^2 = 0.401$. The interaction of Memory and Arousal was not significant.

For reaction times, we report a significant effect of Memory, $F(1, 46) = 85.71, p < 0.001, \eta_p^2 = 0.651$ and Arousal, $F(1, 46) = 13.32, p < 0.001, \eta_p^2 = 0.225$. The interaction of Memory and Arousal was not significant. The behavioural evidence shows that the participants were faster and more accurate on episodic-laboratory retrieval in contrast to semantic retrieval, and, importantly, that they were more accurate and faster on trials that were cued with highly arousing, in comparison to low arousing, images (please see [Fig. 2](#)).

3.2. fMRI results

3.2.1. Whole-brain analysis

The first Task-PLS analysis, which included all four experimental conditions and the control condition, yielded three significant LVs. The first LV differentiated brain activity common to memory conditions from activity during the control condition ($p < 0.001$; accounting for 71% of covariance in the data), confirming that the memory network was engaged regardless of arousal level. The memory network included activity in the superior and inferior frontal gyri, superior and middle temporal gyri, left anterior and posterior cingulate cortex, and right lingual gyrus. In comparison, the control condition activated significantly more the right precentral gyrus, and areas in the middle occipital cortex bilaterally (please see Supplementary Materials, [Fig. 1, Table 1](#); as well as results from LV2 and LV3).

The second Task-PLS yielded two significant LVs and revealed two patterns of brain activity related to the experimental conditions. The first pattern accounted for 70% of covariance in the data and differentiated the episodic-laboratory memory conditions from the semantic memory conditions ($p < 0.001$). In contrast to episodic retrieval, semantic retrieval (regardless of arousal) engaged the left posterior cingulate, middle temporal gyri, left superior frontal gyrus, angular gyrus and lingual gyrus, reflecting the primary nodes of the semantic memory network. In contrast to semantic retrieval, episodic retrieval activated the inferior parietal lobule bilaterally, inferior temporal gyrus, right superior and middle frontal gyrus, and left anterior cingulate, reflecting the primary nodes of the episodic memory network ([Fig. 3 and Table 1](#)).

The second pattern of brain activity from this analysis, accounting for 21% of covariance in the data, delineated the arousal effect, differentiating activity during high negative arousing memory conditions from activity during low arousing memory conditions, independent of memory type ($p < 0.001$). During the high arousing negative, compared to the low arousing neutral conditions, significantly higher activations were found in the parahippocampal gyri and lingual gyri bilaterally,

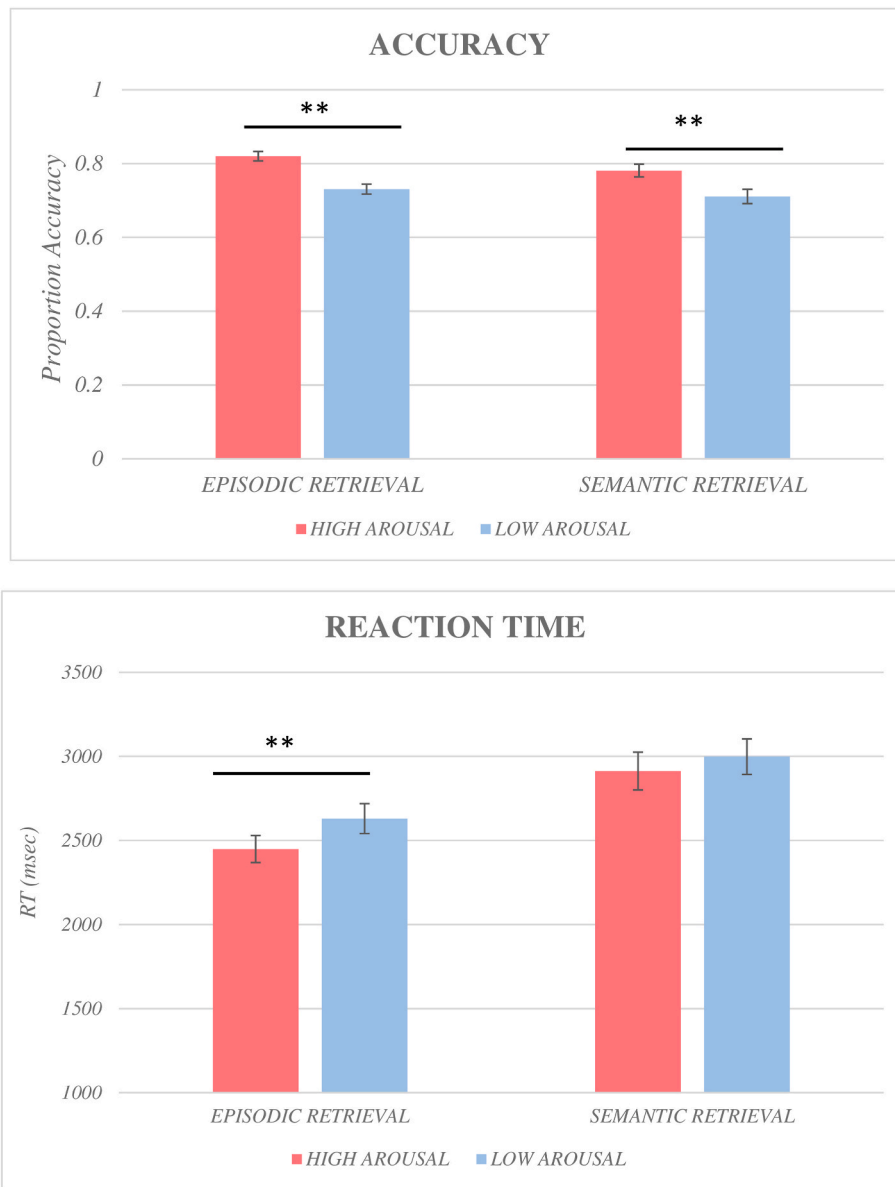


Fig. 2. A) Mean accuracy; B) Mean reaction time (accurate trials only) across the experimental conditions. Error bars represent the standard error. An arousal effect of accuracy is found for episodic and semantic memory retrieval. Participants were significantly faster for the high arousing episodic condition, compared to the low arousing episodic condition. The asterisks denote a statistically significant difference at the $p < 0.01$ level.

right supramarginal and postcentral gyrus, and regions of the middle and superior and medial temporal gyri. In contrast, during the low arousing conditions, significantly higher activations were found in the middle temporal gyri, right inferior temporal gyrus, fusiform gyri, left supramarginal gyrus, inferior frontal gyrus and middle occipital gyri. These results highlight an effect of negative arousal on both episodic and semantic memory (Fig. 4 and Table 2).

3.2.2. Behavioural PLS analysis

The brain-behaviour PLS, relating accuracy and reaction times to whole-brain activity during the experimental conditions revealed one significant LV, which yielded a whole-brain pattern of activity accounting for 32% of covariance in the data ($p < 0.001$). This pattern of activity differentiated performance associated with more accurate and faster responses, from performance related to less accurate and slower responses. Better behavioural performance was coupled with activity in the superior and middle frontal gyri, left postcentral and precentral gyrus, left parahippocampal gyrus, lingual gyrus and insula. Activity in

these regions positively correlated with accuracy (i.e., better performance was associated with more activity in these brain areas) and negatively correlated with reaction times (faster performance was associated with more activity in these brain areas; see Fig. 5 (B) and Table 3). Worse behavioural performance was associated with activity in the left medial, inferior and superior frontal gyri, anterior cingulate, caudate nucleus, right insula, precentral gyrus and lingual gyrus (Fig. 5 (C) and Table 3).

4. Discussion

In the current study, we investigated the effect of negative arousal on episodic-laboratory and semantic memory retrieval in young adults, at the behavioural and neural levels. We employed a novel task that required participants to retrieve episodic and semantic memories when previously cued with a high negative or low neutral arousing stimulus. Given that episodic and semantic memory are highly interactive, and yet differ according to their embedded contextual content, our aim was to

Table 1

Regions significantly activated more during the semantic memory retrieval (both high negative and low arousing conditions), compared to the episodic memory retrieval (both high negative and low arousing conditions), and regions significantly activated more during the episodic memory retrieval (both high negative and low arousing conditions), compared to semantic memory retrieval (both high negative and low arousing conditions).

	Hem	Peak region	MNI coordinates			voxels	BSR
			x	y	z		
<i>Semantic > Episodic</i>	L	Posterior Cingulate	-6	-54	20	7973	15.10
	L	Superior Frontal Gyrus	-14	48	49	6344	13.29
	L	Middle Temporal Gyrus	-42	-64	36	633	8.87
	L	Angular Gyrus	-42	-64	38	881	7.46
	R	Middle Temporal Gyrus	56	0	-20	472	6.88
	R	Fusiform Gyrus	42	-68	-10	986	6.27
	R	Lingual Gyrus	16	-76	8	89	6.00
	<i>Episodic > Semantic</i>	R	Inferior Parietal Lobule	46	-36	48	18484
R		Inferior Frontal Gyrus	48	8	28	1214	-8.39
R		Middle Frontal Gyrus	38	42	20	2126	-7.85
L		Inferior Parietal Lobule	-42	-44	46	1797	-7.35
R		Inferior Temporal Gyrus	56	-54	-6	745	-7.22
R		Superior Frontal Gyrus	22	6	68	387	-6.48
L		Anterior Cingulate	2	-22	28	132	-5.29

Abbreviations: Hem = hemisphere; R = right; L = left; BSR = bootstrap ratio (salience/SE ratio from the bootstrap analysis); x coordinate = right/left; y coordinate = anterior/posterior; z coordinate = superior/inferior.

investigate whether high negative arousal would affect the two memory types similarly. Considering the overlap between episodic and semantic memory, we hypothesised that high negative arousal would be associated with a retrieval advantage (as indicated by better accuracy and faster reaction times, as well as more activity in commonly shared brain regions) for both memory types.

The behavioural results show that participants were better and faster during the high arousing, compared to low arousing trials. This finding is in line with previous evidence supporting an effect of arousal on episodic memory retrieval (e.g., LaBar and Cabeza, 2006; for review Dolcos et al., 2017), and provides novel insights of the arousal effect on semantic memory. We show that the brief exposure to a negative arousing stimulus prior memory retrieval, improves the accuracy and reaction time of both, episodic-laboratory, and semantic memories. This is not surprising given that episodic and semantic memory engage shared processes of a common LTM network (Burianová and Grady, 2007; Burianová et al., 2010). Through the implementation of a single experimental task, which simultaneously examines episodic and semantic memory retrieval, our findings support our hypothesis. The behavioural data provide compelling evidence that heightened negative arousal enhances performance on both types of memories.

Prior to examining novel questions regarding the influence of arousal

on memory retrieval, our first objective was to replicate our previous findings supporting the existence of a common memory network. We report four main findings from the examination of the imaging data. First, the results of the whole-brain analysis showed that episodic high and semantic memory retrieval engaged shared neural processes, which is in line with previous findings supporting the existence of a large-scale unitary memory network (Burianová and Grady, 2007; Burianová et al., 2010). It has been proposed that this overlap arises because episodic memories consist of a combination of familiar concepts and episodic-specific information, with recollection of past episodes prompting not only retrieval of highly contextual details, but also the engagement of conceptual processes (Renoult et al., 2019). In an anti-theoretical manner, semantic memories are rarely entirely context-free (Westmacott and Moscovitch, 2003). For the memory conditions, activated regions included the anterior cingulate cortex, and superior and inferior frontal gyri, implicated in episodic memory retrieval (Nyberg et al., 2003), posterior cingulate and temporal gyri, regions proposed to be part of a core episodic memory network (Rugg and Vilberg, 2012) and lingual gyrus which is found to be functionally connected to the 'core' memory network (Burianová et al., 2010). In contrast, the control condition (and to some extent the episodic low arousing condition), predominantly recruited visual processing regions. This finding is not surprising as the control condition required participants to look at the screen and respond to a simple statement, without prompting any challenging decision-making processes. Finally, we propose that the higher variance observed in the semantic, compared to the episodic conditions, can be attributed to the inherent characteristics of these two memory types. In the semantic condition, participants were not explicitly required to continuously engage with the preceding image, allowing them to potentially "abandon" that cue. In contrast, the episodic memory conditions necessitated active engagement with the image as the subsequent statement directly referred to it.

Our results further reveal distinct patterns of activity related to each of the memory types, supporting unique activations associated with episodic and semantic memory. Semantic, compared to episodic memory retrieval was associated with increased activity in the middle temporal gyri, left posterior cingulate and angular gyrus, right lingual gyrus and left superior frontal gyrus, while episodic memory retrieval was associated with heightened activity in the inferior parietal lobules, right frontal gyrus, left anterior cingulate and right inferior temporal gyrus. It is important to highlight that this differentiation in activity between the two memory types was not related to the arousal level each memory was cued with. Hence, our study further emphasised that episodic and semantic memory show unique patterns of activation. These findings replicate previous works on the differentiated neural processes underlying semantic and episodic memory retrieval (e.g., Burianová et al., 2010; for review Palacio and Cardenas, 2019; Renoult et al., 2019).

Turning our attention to the findings pertaining to the specific objectives of our study, we found an effect of high negative arousal on brain activity during the retrieval of both memory types. High negative, compared to low arousing memory retrieval, was associated with increased activity in the parahippocampal gyri, left lingual gyrus, medial frontal gyri, right supramarginal gyrus and insula. These results replicate previous findings showing increased activity of the parahippocampal and left lingual gyrus during the retrieval of negative emotional information (Osaka et al., 2013). Despite being less frequently addressed in memory research, the right supramarginal gyrus was significantly activated more during the high negative, compared to low arousing conditions at retrieval, suggesting that this region might play an important role during the retrieval of negatively arousing experiences. Given that the parietal cortex has been implicated predominantly in the allocation of attentional resources (Corbetta and Shulman, 2002), activation of the right supramarginal gyrus might suggest that highly arousing information is better remembered due to receiving greater attentional focus. The insula has previously been implicated in subject introspective awareness of both positive and negative feelings (Craig,

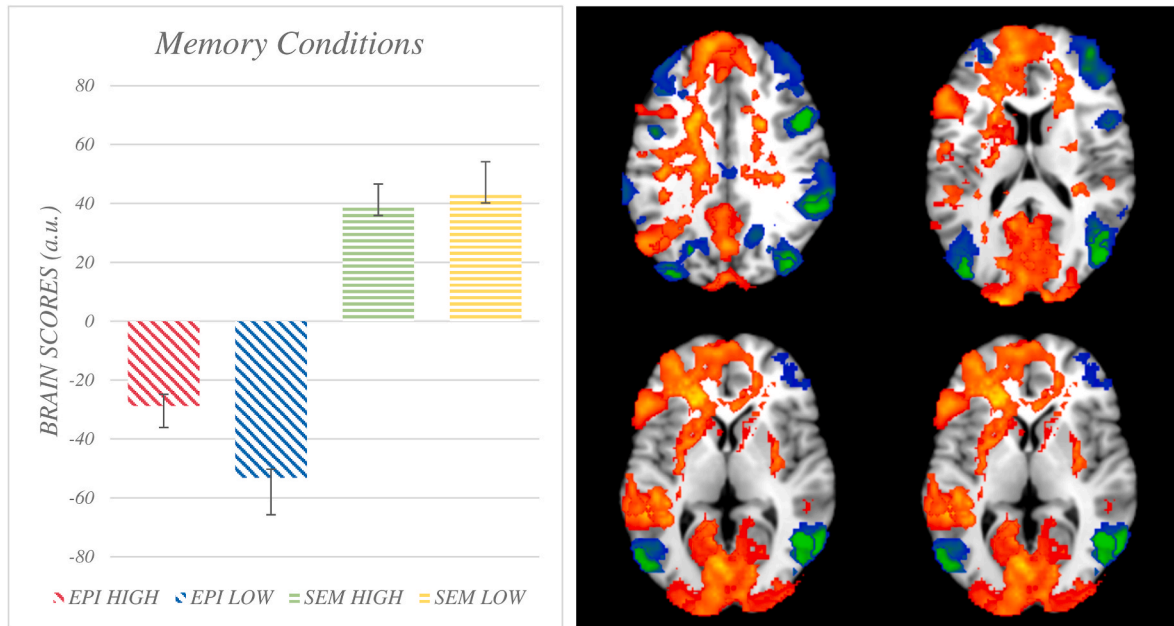


Fig. 3. Task PLS results during memory retrieval on high and low arousing conditions: **(left)** Mean brain scores of the first significant latent variable (LV) across all experimental conditions, related to whole brain activity during memory retrieval (both high and low arousing conditions) versus semantic memory retrieval (both high and low arousing conditions); **(right)** Whole brain activity during episodic and semantic memory retrieval. Activation during semantic memory conditions is represented in red/yellow. Activation during episodic memory conditions is represented in blue/green. Error bars denote 95% confidence intervals calculated from the bootstrap procedure.

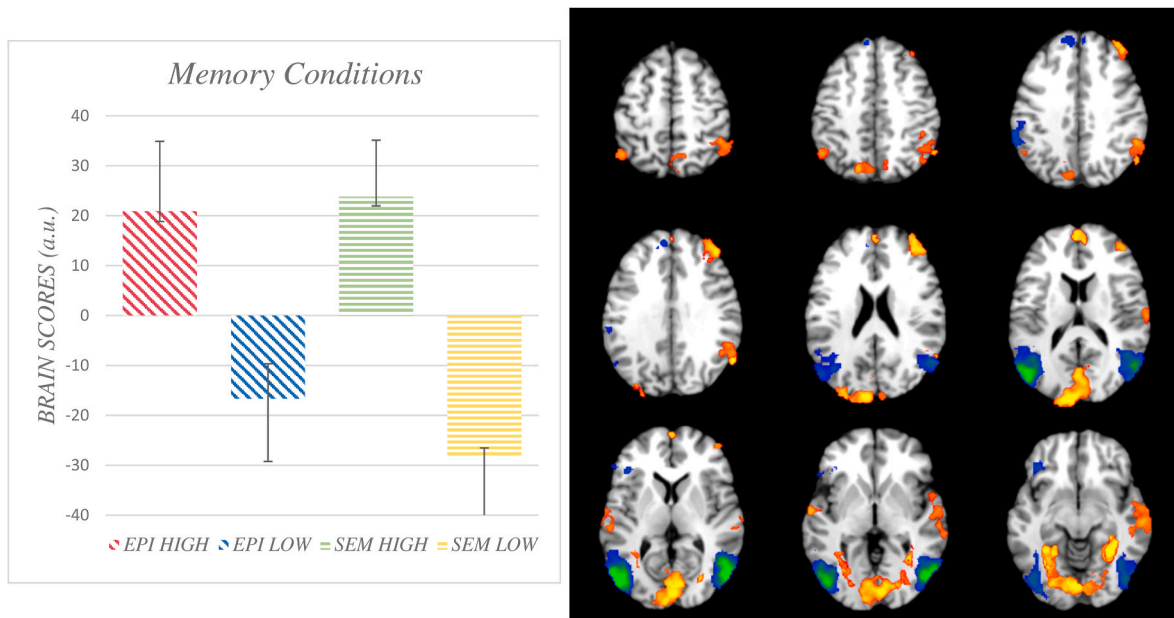


Fig. 4. Task PLS results during memory retrieval on high and low arousing conditions: **(left)** Mean brain scores of the second significant latent variable (LV) across all experimental conditions, related to whole brain activity during memory retrieval cued with a high arousing stimulus versus memory retrieval cued with a low arousing stimulus; **(right)** Whole brain activity during episodic and semantic memory retrieval. Activation during the high arousing memory conditions is represented in red/yellow. Activation during the low arousing memory conditions is represented in blue/green. Error bars denote 95% confidence intervals calculated from the bootstrap procedure.

2002). Considering our study design, activity in the insular cortex might potentially illuminate the subjective awareness provoked by the high negative stimulus, about that negative stimulus. In light of the observed association between better behavioural performance and negative arousing conditions, compared to low arousing conditions, our results potentially indicate the involvement of enhanced binding mechanisms for highly negative information. This suggests that the processing and

integration of highly negative arousing stimuli, may lead to more effective consolidation and retrieval processes, resulting in improved behavioural performance. In line with previous evidence showing hippocampal activity to support binding mechanisms during episodic memory retrieval (e.g., Aminoff et al., 2013; Ranganath, 2010), it is plausible that the observed better performance in negative arousing conditions may be attributed to the increased involvement of the limbic

Table 2

Regions significantly activated more during the high arousing conditions, compared to the low arousing conditions, and regions activated more during the low arousing conditions, compared to the high arousing conditions.

	Hem	Peak region	MNI coordinates			voxels	BSR
			x	y	z		
<i>High Arousing > Low Arousing</i>							
	R	Parahippocampus	28	-44	-8	522	8.35
	L	Parahippocampus	-30	-46	-10	756	7.07
	L	Lingual Gyrus	-26	-62	-2	965	6.52
	R	Supramarginal gyrus	54	-46	36	836	4.99
	R	Medial Frontal gyrus	20	10	66	242	5.65
	L	Medial Frontal Gyrus	0	62	10	204	4.61
	R	Postcentral Gyrus	64	-12	22	118	4.91
	R	Middle Frontal Gyrus	42	42	30	644	5.47
	R	Insula	38	-32	22	139	5.25
<i>Low Arousing > High Arousing</i>							
	R	Inferior Temporal Gyrus	50	-70	0	1795	-11.55
	L	Middle Temporal Gyrus	-54	-64	12	1976	-9.19
	R	Middle Temporal Gyrus	50	-64	6	697	-7.57
	L	Middle Occipital Gyrus	-46	-76	12	638	-7.21
	R	Fusiform Gyrus	42	-50	-14	136	-7.18
	L	Fusiform Gyrus	-42	-50	-14	122	-5.40
	L	Inferior Frontal Gyrus	-36	34	-4	302	-5.08
	L	Supramarginal Gyrus	-58	-36	34	103	-4.41

Abbreviations: Hem = hemisphere; R = right; L = left; BSR = bootstrap ratio (salience/SE ratio from the bootstrap analysis); x coordinate = right/left; y coordinate = anterior/posterior; z coordinate = superior/inferior.

system in the binding of arousing information during retrieval. A distinct pattern of neural activity was observed for the low arousing episodic and semantic conditions, and it included activity in the right inferior and middle temporal gyri, occipital gyrus, fusiform gyri, left inferior frontal and supramarginal gyrus. The engagement of visual processing regions suggests that the retrieval of low arousing episodic and semantic memories may rely heavily on visual and perceptual mechanisms. In addition, the contribution of the fusiform gyri, known for their involvement in face and object recognition (Weiner and Zilles, 2016), may contribute to the visual processing of stimuli associated with low arousal conditions. The activation differences observed between conditions provide valuable insights into the relative involvement and sensitivity of specific brain regions in response to different conditions. It is important, however, to recognise that these activation differences do not imply exclusive involvement or function limited to only one condition. In light of this understanding, we propose that high arousing negative information prompts the engagement of additional regions that may not be as prominently involved during low arousing memory retrieval. The heightened activity of regions associated with the high arousing conditions potentially contributes to the improved behavioural performance observed following the brief exposure to a highly negative arousing stimulus.

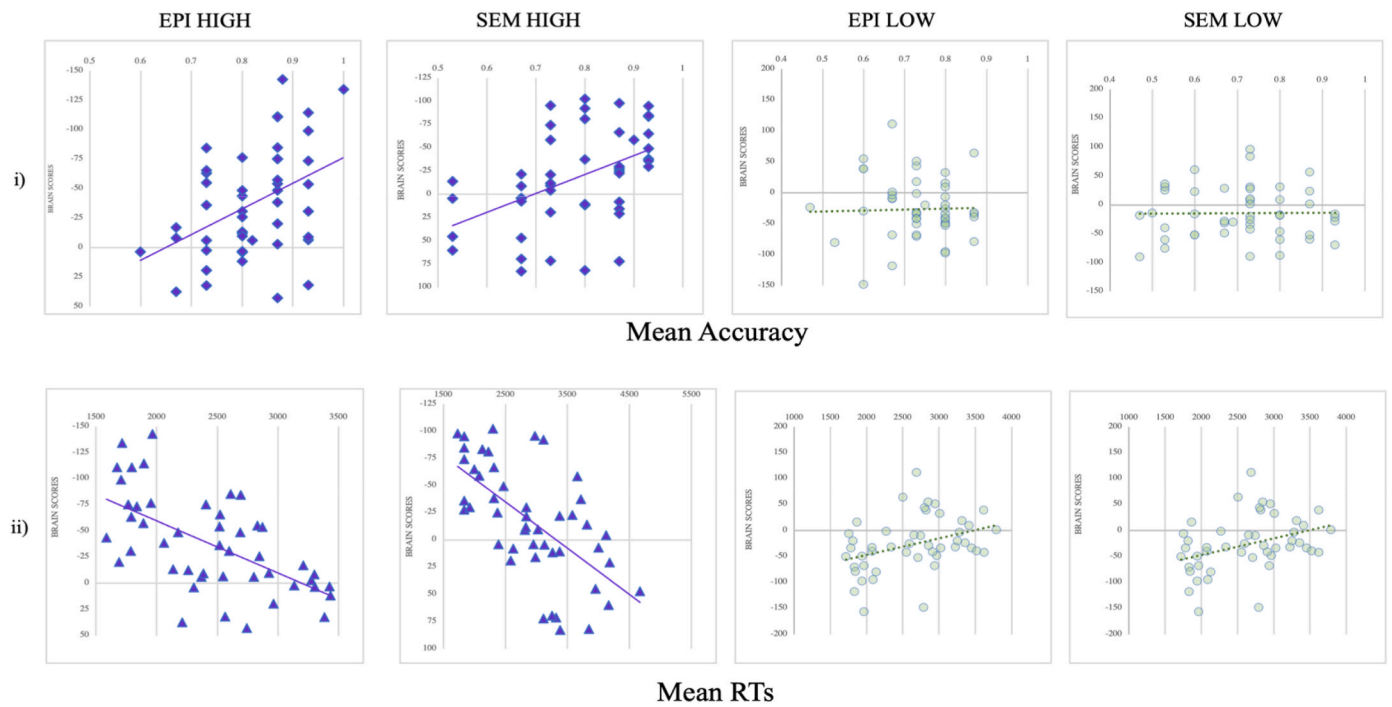
Finally, we established a relation between participants' behavioural performance and brain activity. We found that individuals who exhibited better and faster performance showed increased activation in the left parahippocampal gyrus and insula. This finding indicates the limbic system's involvement in relation to declarative memory retrieval following the presentation of something highly negatively arousing. The parahippocampal gyrus, as a component of the limbic system, has been consistently implicated in memory processing, particularly in the encoding and retrieval of episodic memories (Aminoff et al., 2013). Increased parahippocampal activity in individuals with better performance signals its potential role in the successful retrieval of emotionally arousing information. Similarly, the insula, also part of the limbic system, has been associated with the facilitation of introspective signals and subjective awareness (Gu et al., 2013). The current set of results further emphasises its involvement in the integration of emotional negative content with memory retrieval processes.

Here, it is important to clarify that the absence of significant hippocampal activity in our study does not necessarily imply its lack of activation. Instead, our PLS results signify that no statistically significant differences were detected in hippocampal activity between conditions.

Further region of interest analyses may shed light on potential hippocampal involvement in our experimental paradigm. Moreover, we found increased activity in the left posterior cingulate cortex, which aligns with previous findings highlighting its engagement in memory processes (Rolls, 2019). The right frontal gyrus and right middle temporal gyrus were also found to be associated with better performance. The second neural pattern was associated with poorer accuracy and slower response times and included activity in the frontal cortex, specifically in the superior frontal gyrus, right precentral and lingual gyrus. Furthermore, we observed that the right insula showed preferential activity for lower performance (whereas the left insula showed increased activity in higher performing individuals). This finding complements the existing body of evidence that underscores the distinct contributions of the left and right insular cortex (Scalabrini et al., 2021). Finally, activity in the anterior cingulate cortex might potentially signal error detection awareness (e.g., Orr and Hester, 2012). These findings not only replicate the impact of high negative arousal effect on episodic and semantic memory retrieval, but also demonstrate that different brain regions are engaged based on variations in behavioural performance. Specifically, certain regions exhibited increased activity in response to better performance, while others showed altered activity in association with poorer performance. Together, these findings provide compelling empirical evidence supporting the heightened neural activity associated with negative arousal during declarative memory retrieval.

It is noteworthy to address some potential limitations of our study that warrant consideration. Firstly, the use of negative images to induce arousal raises the possibility that the observed effects may be influenced by the negative valence associated with these highly arousing stimuli. Consequently, it remains uncertain whether the observed effects can be generalized to arousal accompanying positive images, or is they are specific to negative valence. Additionally, while we implemented a controlled comparison between negative and neutral images by randomizing the order of image presentation, we did not directly address potential repetition effects of duplicated images. Although randomization aimed to minimize any potential bias in the observed variance between the two conditions and ensure differences could be attributed to the arousal manipulation, it is important to note the potential presence of priming effects and their interaction with arousal levels. Future studies should consider addressing these limitations by including positive arousing stimuli, controlling for valence-related effects, and exploring potential repetition effects to provide a more comprehensive understanding of the specific influences of valence,

A)



B) Brain activity related to better task performance

C) Brain activity related to worse task performance

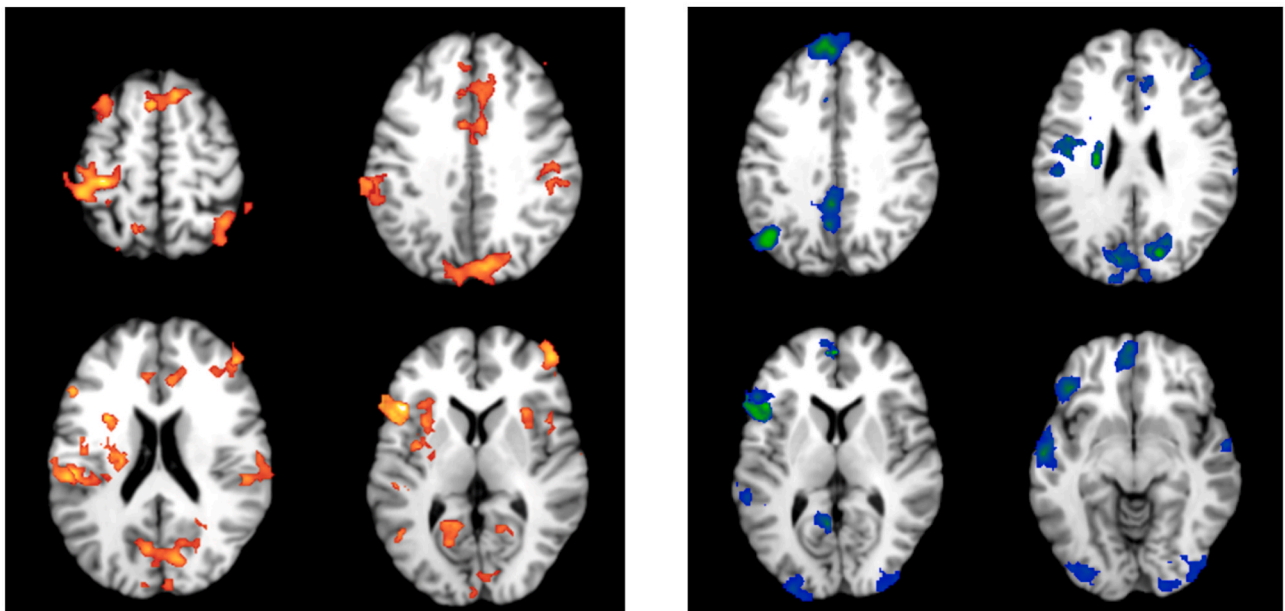


Fig. 5. Results of the Behavioural PLS analysis. A) Correlations between participants’ whole-brain activity and behavioural measures of accuracy and reaction times per condition. Scatterplots show the relationship between averaged individual brain scores and i) accuracy and ii) reaction time scores for episodic and semantic memory retrieval. B) Regions corresponding to areas activated more during better and faster task performance are highlighted in yellow/red. C) Regions activated more during worse and slower task performance are highlighted in blue/green.

arousal, and repetition on memory retrieval processes. By doing so, we can further enhance the validity and generalizability of our findings. Another crucial consideration we wish to highlight concerns the potential contribution of the working memory system in accounting for certain aspects of our findings. Although this was not the primary focus of the present study, we acknowledge the significance of recognizing that some of our observed outcomes may be attributed, at least in part,

to the engagement of working memory. The extended presentation duration of the images in our paradigm, surpassing that typically seen in conventional working memory tasks, coupled with the context-rich nature of the stimuli, strongly suggests a predominant reliance on episodic memory. Nonetheless, it is imperative to acknowledge that the influence of working memory cannot be entirely discounted.

Additionally, we would like to emphasise the significance of

Table 3

Significantly increased activations associated with more accurate and faster responses, compared to less accurate and slower responses and significantly increased activations associated with less accurate and slower responses, compared to more accurate and faster responses.

	Peak region	MNI coordinates			voxels	BSR
		z	y	z		
<i>Higher ACC & RTs > Lower ACC & RTs</i>						
L	Postcentral Gyrus	-32	-28	42	2764	9.72
L	Insula	-50	-24	20	241	6.73
L	Parahippocampus	-14	-50	4	2298	6.71
R	Middle Frontal Gyrus	46	50	10	599	6.08
L	Posterior Cingulate	-28	-72	14	2208	6.02
L	Lingual Gyrus	-8	-90	-12	402	4.72
R	Medial Frontal Gyrus	8	64	4	165	3.90
R	Middle Temporal Gyrus	68	-6	-18	260	3.40
<i>Lower ACC & RTs > Higher ACC & RTs</i>						
L	Medial Frontal Gyrus	-8	16	46	214	-6.71
L	Inferior Frontal Gyrus	-46	20	8	438	-5.59
R	Insula	32	26	4	50	-5.53
R	Superior Frontal Gyrus	4	20	48	438	-5.32
L	Anterior Cingulate	-8	46	-4	104	-4.40
L	Caudate	-36	-26	-8	1044	-4.21
R	Precentral Gyrus	54	2	48	410	-4.12
R	Lingual Gyrus	28	-74	0	351	-3.96
L	Superior Frontal Gyrus	2	22	48	741	-3.84

Abbreviations: Hem = hemisphere; R = right; L = left; BSR = bootstrap ratio (salience/SE ratio from the bootstrap analysis); x coordinate = right/left; y coordinate = anterior/posterior; z coordinate = superior/inferior.

investigating the arousal effect of negative stimuli in healthy ageing. Considering that older adults often display a positivity effect, where they exhibit a bias towards processing positive information (Charles et al., 2003; Mammarella et al., 2016) and possibly decrease the prioritization of negative stimuli (e.g., Sasse et al., 2014), it becomes intriguing to explore whether the same arousal effect persists in this population. It would be captivating to examine whether older adults are more inclined to disregard negative stimuli compared to younger adults, and whether this would be accompanied with differences in behavioural and neural performance. Further research in this area becomes even more compelling when considering the dissociation often observed between episodic and semantic memory in older adults (e.g., Spaniol et al., 2008). As our study explored the effects of arousal on both memory types, it would be valuable to examine whether older adults demonstrate similar or divergent patterns compared to younger adults in terms of the influence of arousal on episodic and semantic memory retrieval. Understanding how arousal interacts with memory systems in the context of healthy ageing could provide valuable insights into the underlying mechanisms of age-related memory changes and potentially inform interventions to support memory function in older individuals.

Overall, our study provides evidence supporting previous findings on the existence of a common LTM network and extending these by a novel finding of an arousal effect on episodic and semantic memory retrieval. By analyzing the relationship between behavioural performance and the corresponding neural patterns, we aimed to gain a deeper understanding of the underlying mechanisms that govern memory retrieval processes following brief arousal exposure. Brief exposure to highly negative arousing images was found to be accompanied by a better and faster memory retrieval performance in young adults, not only for episodic, but also semantic information, and an increase in neural activity during

the retrieval of high arousing negative information. Our work makes a significant contribution to current research by investigating the impact of varying levels of arousal during retrieval on two distinct types of memory. By considering the dynamic nature of brain functioning and the complex interplay between different regions, we gain a more comprehensive understanding of how cognitive processes are supported. These findings shed light on the nuanced mechanisms underlying declarative memory retrieval in the context of arousal, paving the way for further investigations.

Author contributions

MC, KK and HB: wrote the manuscript, data collection, data analysis; HB and LM: study design, data collection, data quality check, data analysis; HB: developed fMRI protocol, fMRI data quality check; All authors have read and agreed to the published version of the manuscript.

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Institutional review board statement

The study was reviewed and approved by the Departmental Research Board and Ethics Committee at Swansea University.

Informed consent statement

All participants provided informed consent.

Declaration of competing interest

The authors declare no conflict of interest.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuropsychologia.2023.108759>.

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