



Typicality in the brain during semantic and episodic memory decisions

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ABSTRACT

Concept typicality is a key semantic dimension supporting the categorical organization of items based on their features, such that typical items share more features with other members of their category than atypical items, which are more distinctive. Typicality effects manifest in better accuracy and faster response times during categorization tasks, but higher performance for atypical items in episodic memory tasks, due to their distinctiveness. At a neural level, typicality has been linked to the anterior temporal lobe (ATL) and the inferior frontal gyrus (IFG) in semantic decision tasks, but patterns of brain activity during episodic memory tasks remain to be understood. We investigated the neural correlates of typicality in semantic and episodic memory to determine the brain regions associated with semantic typicality and uncover effects arising when items are reinstated during retrieval. In an fMRI study, 26 healthy young subjects first performed a category verification task on words representing typical and atypical concepts (encoding), and then completed a recognition memory task (retrieval). In line with previous literature, we observed higher accuracy and faster response times for typical items in the category verification task, while atypical items were better recognized in the episodic memory task. During category verification, univariate analyses revealed a greater involvement of the angular gyrus for typical items and the inferior frontal gyrus for atypical items. During the correct recognition of old items, regions belonging to the core recollection network were activated. We then compared the similarity of the representations from encoding to retrieval (ERS) using Representation Similarity Analyses. Results showed that typical items were reinstated more than atypical ones in several regions including the left precuneus and left anterior temporal lobe (ATL). This suggests that the correct retrieval of typical items requires finer-grained processing, evidenced by greater item-specific reinstatement, which is needed to resolve their confusability with other members of the category due to their higher feature similarity. Our findings confirm the centrality of the ATL in the processing of typicality while extending it to memory retrieval.

1. Introduction

Semantic and episodic memory are two declarative long-term memory systems known to interact very closely (Tulving, 1972, 1985). The former holds our semantic knowledge about the world, abstracted away from our experiences (e.g., the meaning of words) and applied to a variety of contexts. The latter instead refers to episodic events personally experienced in the past, which emerges from the binding of information that co-occurred in the specific context where the event took place. Even though the independence of these two systems is supported by neuroimaging and clinical evidence (Tulving, 1972, 1985), they also demonstrate an interplay. Semantic processing may, for example,

enhance episodic retrieval (e.g., levels of processing and semantic congruency effects, Bartlett, 1932; Craik and Lockhart, 1972) as well as hinder episodic remembering (e.g., giving rise to false memories; see Greenberg and Verfaellie, 2010 for review). Thus, the idea of a neat separation between episodic and semantic systems has been recently questioned, because these two systems seem to be supported by partially overlapping brain networks and common retrieval processes (Greenberg and Verfaellie, 2010; Irish and Vatansver, 2020; Renoult et al., 2019).

One of the most integrative theoretical accounts of semantic memory, the Hub-and-Spoke model (Patterson et al., 2007; Ralph et al., 2017), holds that semantic categories arise from intrinsic regularities among conceptual features of objects. In particular, the anterior

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temporal lobe (ATL), which includes the temporal gyri, temporal pole, rhinal cortices, fusiform and parahippocampal gyri (Bonner and Price, 2013), works as a semantic hub where conceptual information is amodally integrated and abstractions or generalizations across categories are formed. Yet, it remains unclear how the natural variability in the conceptual features of items of the same category is represented by the human brain, with some authors relating it to their typicality (Santi et al., 2016; Woollams, 2012; Woollams et al., 2008). Indeed, a key property of concepts is their graded category membership, according to which some members are more typical, or a better exemplar of the category than others (Rosch and Mervis, 1975). Within a given category (e.g., bird), a typical item (e.g., sparrow) shares many features with the other members of its category while, conversely, an atypical item (e.g., penguin) is characterized by more idiosyncratic features, making atypical items more distinctive within their category. Hence, according to some authors, typicality reflects the conceptual structure as expressed by the co-occurrence of features between concepts within a given category (Raposo et al., 2012).

Behaviorally, typical items are systematically associated with faster response times and lower error rates than atypical items in naming (Holmes and Ellis, 2006) and category verification tasks (Kiran et al., 2007). However, at a neural level, results are more inconsistent, which may be partly due to the different tasks used (i.e., naming, categorization, feature verification) or the stimuli adopted (words vs. pictures; e.g., see Davis and Poldrack, 2014; Jordan et al., 2016; Li et al., 2021). On one hand, studies on patients with semantic dementia (SD), presenting with ATL atrophy (Woollams et al., 2008), and with healthy controls following Transcranial Magnetic Stimulation (TMS) on the ATL (Woollams, 2012), showed that disruption of the ATL leads to impairments in naming tasks for more atypical concepts, which aligns with fMRI studies on healthy participants showing increased activation in the ATL with decreasing item typicality during a category verification task (Santi et al., 2016). On the other hand, studies using Representational Similarity Analysis (RSA, Kriegeskorte et al., 2008) demonstrated that in the ATL region, the semantic similarity between concepts (as measured in terms of shared and distinctive feature norms) matches voxel similarity patterns elicited by objects processed semantically (Borghesani et al., 2016; Bruffaerts et al., 2013; Chen et al., 2016; Clarke, 2020; Clarke and Tyler, 2014; Fairhall and Caramazza, 2013; Liuzzi et al., 2015; Martin et al., 2018). Taken together, these results support the idea that concepts are processed and represented in the ATL through the integration of their constituting features, both shared and distinctive ones (Bruett et al., 2020; Bruffaerts et al., 2019; Coutanche and Thompson-Schill, 2015).

Beyond the ATL, researchers have identified a supramodal left-lateralized network, comprising the posterior middle/inferior temporal gyrus, angular gyrus (AG), ventral temporal cortex, precuneus (PC), and lateral and dorsomedial prefrontal cortex, representing semantic content during a typicality judgement task (Fairhall and Caramazza, 2013). In addition, imaging work on semantic categorization of items varying in typicality has revealed increased activation in the inferior frontal gyrus (IFG) for more atypical items, whereas typical items displayed enhanced activation in the inferior parietal and posterior temporal regions (Santi et al., 2016). These findings are corroborated by a recent fMRI study demonstrating that, in addition to the ATL, the left IFG was significantly more recruited during the processing of distinctive (e.g., has a mane) than shared features (e.g., has four legs) of concepts, whereas the right AG revealed the opposite pattern (Reilly et al., 2019). Together, these results suggest that processing atypical items, which possess more distinctive features, requires greater semantic control possibly due to the lower feature co-occurrence (Santi et al., 2016). Conversely, inferior parietal regions, including the AG, are engaged in similarity-based categorization (Grossman et al., 2002), and possibly function as another cross-modal semantic hub, integrating semantic features within a single concept or across concepts to relate with broader memory and cognitive processes (Bonner et al., 2013; Bonnici et al.,

2016; Farahibozorg et al., 2022; Seghier, 2013).

Understanding how the organization of semantic memory influences episodic memory mechanisms remains of key concern, especially considering that little is yet known about the role that typicality plays in it. Only a few studies have explored this issue and they consistently showed that atypical items are associated with better recognition memory than typical ones, and this difference may be attributed to increased recollection rather than familiarity (Alves and Raposo, 2015; Souza et al., 2021). One interpretation of this effect is that atypical items are more distinctive, because of their idiosyncratic features compared to other members of their category (e.g., a penguin among typical birds; Hunt, 2013; Tulving and Rosenbaum, 2006), which may have beneficial effects on episodic memory encoding (von Restorff, 1933). The impact of typicality on subsequent memory has also been studied in the context of expectancies, or predictions. In the presence of a category-cue, expectations would build up towards typical items, while atypical items, that are unexpected, elicit a mismatch between the presented stimulus and the prediction (Federmeier et al., 2010). Such mismatch detection can benefit subsequent memory (Federmeier et al., 2007; but see Höljtje et al., 2019).

Whether concept typicality affects the neural correlates of successful memory retrieval has never been explored. To address this question, we used fMRI in both a semantic categorization task during encoding of typical and atypical items and a subsequent recognition memory task. We first conducted contrast analysis to inspect the effects of typicality on the neural bases of semantic category verification. We anticipated that the categorization of atypical items should be associated with greater ATL and IFG activation, while for typical items, we expected greater engagement of the right inferior parietal lobe including the AG (Reilly et al., 2019; Santi et al., 2016; Woo et al., 2014). Next, we explored if typicality impacts concept recognition, by contrasting old vs. new items that were typical or atypical members of the category. In complement, we conducted RSA to test if the neural patterns of semantic processing at encoding were reinstated differently for typical and atypical items during retrieval, both at the whole-brain level, and using Region of Interest (ROI) analysis focusing on the ATL. One hypothesis is that atypical concepts (relative to typical ones) will reveal higher similarity from encoding to retrieval due to their greater distinctiveness which results in greater item-specific reinstatement. Alternatively, since typical concepts are more similar to other members of the category and hence more confusable, their correct retrieval may involve fine-grained processing, which could instead lead to greater item-specific reinstatement, which we expect to occur in the left ATL.

2. Methods

2.1. Participants

26 young healthy adults took part in this fMRI study (20 females, $M = 21.46$ years old ($SD = 3.57$), range = 18–29). All subjects were right-handed, native speakers of Portuguese, and had no history of neurological impairment or head injury. Participants took part in the study in exchange for course credits. They all gave informed written consent to the experimental procedure, which was approved by the ethics committee of Faculdade de Psicologia, Universidade de Lisboa.

2.2. Materials and procedure

We selected 160 words from 10 categories, so to have 16 items per category (fruit, vegetable, bird, insect, mammal, vehicle, musical instrument, clothing, weapon, kitchen utensil). Half of the words consisted of typical members of their category, while the other half were atypical members of their category. Typicality was determined in a previous pretest (see Santi et al., 2016) with an independent group of participants who judged how typical an exemplar for a given category is on a 7-point scale (1 = very typical to 7 = very atypical).

During encoding, participants saw 80 words (40 typical and 40 atypical) for which they were instructed to perform a category verification task. Half of the words were presented with the actual category they belong to, so that they were part of a “congruent” condition (20 typical, 20 atypical), while the other half were presented with an incongruent category (20 typical, 20 atypical). So, our design included 4 conditions: congruent typical, congruent atypical, incongruent typical and incongruent atypical. Items in the typical and atypical conditions differed in terms of typicality ratings ($t(17.19) = 42.92, p < .001$). All conditions were matched in familiarity (all $ps > .30$) and number of letters (all $ps > .29$; see Table 1). To respect the matching of these variables across conditions, items could not be counterbalanced across conditions. Each trial began with the presentation of a fixation cross for 500 ms followed by the category cue (prime) for 750 ms. The prime was followed by a 200 ms blank screen, and the target concept was then presented for 2000 ms, during which participants had to perform the category verification task, by pressing the left index finger for “yes” and the left middle finger for “no”. The target was followed by a jittered 1500–3000 ms blank screen, ending the trial (see Fig. 1).

During retrieval, participants were presented with the 80 words they saw during encoding, and an additional 80 new words, half of which were typical members of their category, and the other half, atypical members. New words were matched with the old words in terms of the category they belong to, typicality ratings, familiarity ratings and number of words ($ps > .1$ in all cases; see Table 1). Participants were asked to determine whether they saw the item previously in a yes-no recognition task by pressing the same keys as during encoding, and then to judge the confidence of their answer on a 4-point scale (using the left hand). Each trial started with a fixation cross presented for 500 ms followed by the probe (target concept) for 2500 ms, during which participants had to determine whether the item was old or new. The probe was followed by a 200 ms blank screen, after which the screen displayed the confidence judgement scale for 2000 ms during which participants were asked to provide their confidence judgement. The trial ended with a jittered 2000–3500 ms blank screen. The order of presentation of the words was randomized across participants. Both the category verification task and the recognition phases were performed in the scanner. See Fig. 1 for an example of the design of the tasks.

2.3. MRI data acquisition and preprocessing

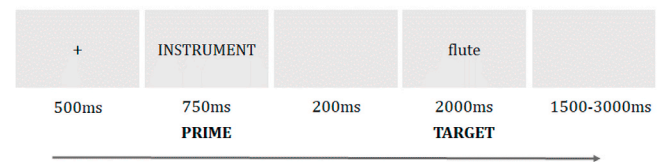
Scanning was conducted at Sociedade Portuguesa de Ressonância Magnética on a 3 T Philips MR system (Philips Medical Systems, Best, NL) using a standard head coil. Functional data were acquired by using an echo-planar sequence (TR = 2000 ms, TE = 23 ms, FA = 90°, FOV = 230 × 230 mm, 34 bottom-up interleaved slices parallel to the AC-PC line, with 1.8 × 1.8 × 3.5 mm voxels size, matrix size = 116 × 115). Acquisition covered the entire brain. Before functional data collection, three dummy volumes were discarded to allow for T1 equilibrium. High-resolution T1-weighted anatomical images were acquired for visualization and spatial processing of the fMRI (coregistration and normalization).

The fMRI data were preprocessed and statistically analyzed using Statistical Parametric Mapping toolbox (SPM12, Wellcome Institute of Cognitive Neurology, www.fil.ion.ucl.ac.uk) within Matlab (version

Table 1
Descriptive statistics (mean, and SD in brackets) of the stimuli characteristics.

		Number of letters	Familiarity (1–7)	Typicality (1–7)
Typical	Congruent	6.65 (2.28)	4.20 (1.03)	6.68 (0.20)
	Incongruent	6.10 (2.07)	4.16 (1.41)	6.70 (0.22)
	New	6.42 (1.65)	4.02 (1.07)	6.54 (0.30)
Atypical	Congruent	6.45 (1.96)	3.93 (0.96)	4.08 (0.93)
	Incongruent	7.00 (2.90)	4.46 (1.15)	4.10 (0.96)
	New	7.02 (3.47)	4.33 (1.17)	4.12 (1.08)

Encoding (scanned) – category verification task



Retrieval (scanned) – old/new recognition memory task

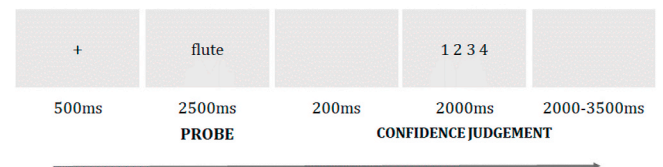


Fig. 1. Experimental task. Top: category verification task for typical and atypical items, bottom: recognition memory task where old congruent items from the category verification task were interspersed among new typical and atypical items from the same categories.

2015b, Mathworks Inc., Sherborn MA, USA). First, we corrected for differences in slice acquisition timing by resampling all slices to the middle slice. These data were then corrected for motion across all sessions by aligning to the mean of the images collected after the first realignment. The mean resliced functional data were coregistered to the participants’ T1. The T1 was then segmented in order to obtain the normalization parameters. Voxel size was resampled into isotropic 2 × 2 × 2 mm. The normalization parameters were then applied to the pre-processed functionals. Normalized functional data were then spatially smoothed with an isotropic Gaussian kernel of 8 mm FWHM.

2.4. Behavioral data analyses

Data from the encoding category verification task were analyzed using a repeated-measures ANOVA with congruency (congruent, incongruent) and typicality (typical, atypical) as within-subject variables on the proportion of correct answers and on the response time for correct trials. As for the recognition task, we ran repeated measures ANOVAs on the hit rates, hits with high confidence responses only (level 4), false alarm rates (FAs), and hits-FAs global accuracy measure. The repeated measures ANOVAs on the hit rates and the hits-FAs accuracy measure included congruency between the target and the prime during the encoding category-verification task (congruent, incongruent) as well as typicality (typical, atypical) as within-subject factors. The repeated-measures ANOVA on the FAs included typicality (typical, atypical) as the within-subject factor.

2.5. fMRI data analyses

2.5.1. Univariate analyses

For each participant, BOLD responses were modelled using the General Linear Model (GLM) implemented in SPM12. In the category verification task, regressors of interest were modelled as epochs that began when the prime (category cue) was presented and finished before the onset of the next prime (4.95–6.45 s). The design matrix included 4 regressors: typical targets that were congruent with the prime, atypical targets that were congruent with the prime, typical targets that were incongruent with the prime, atypical targets that were incongruent with the prime.

The analysis of the recognition memory task focused on trials associated with a correct response (i.e., accurate recognition) as several studies have reported neural differences as a function of retrieval success (e.g., Herron et al., 2004). Regressors of interest were modelled as epochs that began with the onset of the probe and finished before the onset of the next probe (7.2–8.7 s). The design matrix included 6

regressors: old items from the congruent typical condition, old items from the congruent atypical condition, new typical items, new atypical items, old items from the incongruent condition and incorrect responses. We included only one regressor for all incongruent trials as this condition led to relatively low levels of recognition accuracy (incongruent typical: $M = 0.56$, $SD = 0.18$; incongruent atypical: $M = 0.64$, $SD = 0.17$), with lower confidence in producing correct responses (see Behavioral results section). Hence, there were not enough correct trials to conduct further analyses on these items. Each design matrix included realignment as nuisance parameters to model movement-related variance.

At the individual subject level (first level), we generated a contrast for each condition of interest versus rest, used as a baseline. The contrast images were then submitted to a second-level analysis corresponding to a random effects model in which subjects were considered as random variables, using factorial ANOVAs in SPM12, and follow-up pairwise comparisons between conditions were implemented using two-sample t -tests. Data from the category verification task were analyzed in a factorial ANOVA, with congruency (congruent, incongruent) and typicality (typical, atypical) as factors. As for the recognition task, we conducted a factorial ANOVA, with probe status (old, new) and typicality (typical, atypical) as factors.

The significance voxel-level threshold was set at $p < .001$, uncorrected, with clusters significant at $p < .05$ (FWE cluster corrected), to correct for multiple comparisons (following recommendations from Woo et al., 2014).

2.5.2. Multivariate analyses

Beta extraction. The preprocessed unsmoothed fMRI images were used to estimate the beta for each trial using the general linear model framework. For each participant and separately for encoding and retrieval, a GLM was constructed that included separate regressors for each individual trial, along with regressors indexing head motion as nuisance parameters. Each trial was modelled as a 0-duration event (see Folville et al., 2020; Wing et al., 2015) and was convolved with a canonical hemodynamic response function. The resulting beta estimates for each trial were then used for subsequent multivariate searchlight analyses using the CoSMoMVA toolbox (Oosterhof et al., 2016).

Searchlight analyses. A whole-brain searchlight approach (Kriegeskorte et al., 2008) was used to calculate the Encoding-Retrieval Similarity (ERS) at the item level by matching individual trials presented at retrieval to their identical counterparts at encoding (e.g., “flute” encoding x “flute” retrieval), and at the set level by matching an individual trial at retrieval to all other stimuli from encoding (e.g., “piano” encoding x “flute” retrieval). For both item-level and set-level pairs, only old items were considered. The set level refers to the general reactivation of concept processing, while the item level refers to the specific reactivation of a given concept. See Fig. 8D for an illustration of the ERS matrix.

For item-level ERS, a $3 \times 3 \times 3$ voxels cube around each voxel of each trial was extracted (from beta maps during encoding and retrieval) and vectorized. Then, the encoding and retrieval vectors were correlated and the resulting value (Fisher-transformed Pearson’s r , our measure) was placed in the original voxel location. This process was repeated for all brain voxels for every item-level pair (mean number of item-level pairs by subject = 32.82, $SD = 3.79$ (because incorrectly identified “old” items were not included in the analysis)). In the set-level ERS, the procedure was similar except that the ERS value at each voxel for a given retrieval trial was the average of many set-level pairs. Specifically, for each retrieval trial (e.g., flute), ERS was calculated separately for all encoding trials from the set (e.g., piano x flute, sparrow x flute, coat x flute, etc.; mean number of pairwise comparisons by subject in the set level = 512.79, $SD = 115.09$) and these different ERS values were averaged for each voxel to create the whole-brain similarity volume for that retrieval trial (Wing et al., 2015). So, for each retrieval trial, we had one value of item-level ERS, and one value of set-level ERS, in each brain voxel.

Statistical analyses. After calculation of item-level and set-level ERS volumes for each retrieval trial, ERS volumes were averaged across trials from the same condition (typical or atypical) at the subject-level, so that each subject ended up with 4 maps: item-level typical, item-level atypical, set-level typical, and set-level atypical. Then, at the group level, we ran a full factorial design in SPM12. We conducted a 2 typicality (typical, atypical) by 2 levels (item, set) factorial ANOVA on ERS maps. Following the same criteria of the univariate analysis, we restricted the analysis to items that were presented with a congruent category cue during learning and accurately recognized at test (mean number of trials, typical = 15.61, atypical = 17.22). We used a cluster-defining threshold of $p < .001$ with clusters significant at $p < .05$ (FWE cluster corrected, Bird et al., 2015; Oedekoven et al., 2017).

In addition to the whole brain analysis, we ran a supplementary ROI analysis that focused specifically on the left ATL since, as discussed at the outset, the ATL is a core region in processing item typicality and is known to be susceptible to signal distortion and signal loss in fMRI because of its position near the sinuses (Olman et al., 2009; Visser et al., 2010). For that, we used the Marsbar toolbox in SPM (Brett et al., 2002), and defined a 10 mm-radius sphere around coordinates reported in a previous independent study assessing ERS using an ATL ROI at $-41, 8, -17$ (Bruett et al., 2020; see also Coutanche and Thompson-Schill, 2015). The same 2 typicality (typical, atypical) by 2 levels (item, set) factorial ANOVA was run on ERS maps within this ROI.

3. Results

3.1. Behavioral results

3.1.1. Category verification task

The repeated measures ANOVA on the proportion of correct answers with congruency (congruent, incongruent) and typicality (typical, atypical) as within-subject factors was characterized by a main effect of congruency, $F(1,25) = 31.79$, $p < .001$, $\eta_p^2 = .56$, with better performance for incongruent than congruent targets. There was also a main effect of typicality, $F(1,25) = 43.76$, $p < .001$, $\eta_p^2 = .64$, with more accurate categorization of typical than atypical items. The congruency \times typicality interaction was also significant, $F(1,25) = 64.43$, $p < .001$, $\eta_p^2 = .72$, according to which, for the incongruent condition, there was no difference in categorization accuracy between typical and atypical items ($p = 1.00$, Bonferroni post-hoc test), while in the congruent condition, categorization was significantly better for the typical than atypical items ($p < .001$) (see Fig. 2).

Regarding response times, we found a main effect of typicality, $F(1,25) = 57.29$, $p < .001$, $\eta_p^2 = .68$, with typical items leading to faster responses than atypical items. There was no main effect of congruency, $F(1,25) = 0.83$, $p = .37$, $\eta_p^2 = .03$, but there was a significant interaction between congruency and typicality, $F(1,25) = 25.00$, $p < .001$, $\eta_p^2 = .48$, showing no difference in response time between typical and atypical items in the incongruent condition ($p = .41$), while typical items led to faster response times than atypical items in the congruent condition ($p < .001$).

3.1.2. Recognition memory task

The ANOVA on hit rates with congruency (congruent, incongruent) and typicality (typical, atypical) as within-subject variables revealed that congruency at encoding impacted subsequent recognition, with higher hit rates for items that were congruent with the presented category than incongruent ones, $F(1,25) = 80.19$, $p < .001$, $\eta_p^2 = .76$. There was also a main effect of typicality, with higher hit rates for atypical than typical items, $F(1,25) = 11.84$, $p = .002$, $\eta_p^2 = .32$. The interaction between congruency at encoding and typicality was not significant, $F(1,25) = 0.01$, $p = .95$, $\eta_p^2 = .01$. The same analysis on high confidence responses only (level 4 of confidence) revealed the same pattern of results, with the main effect of congruency showing more hits for congruent than incongruent items, $F(1,25) = 171.45$, $p < .001$, $\eta_p^2 = .87$,

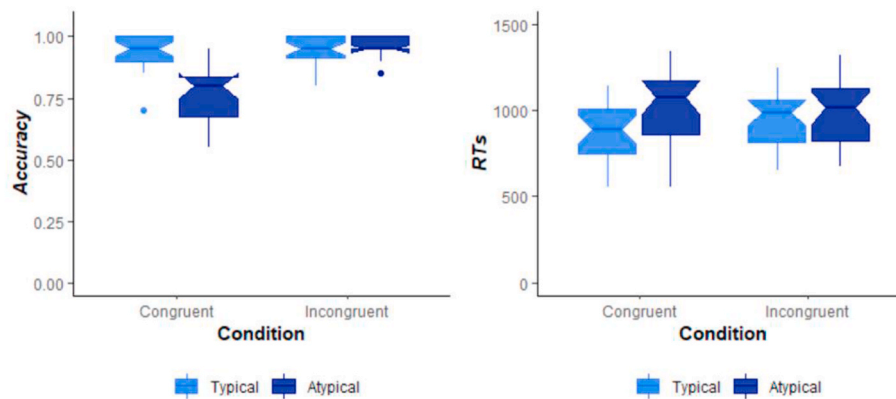


Fig. 2. Accuracy (left) and response times for correct trials (in ms, right) in the category verification task for congruent and incongruent trials across conditions of typicality.

a main effect of typicality with more high confidence hits for atypical than typical items, $F(1,25) = 48.81, p < .001, \eta_p^2 = .66$, and no interaction between congruency and typicality, $F(1,25) = 0.01, p = .95, \eta_p^2 = .01$ (Table 2). There was a significantly greater proportion of false alarms in the typical than atypical condition, $F(1,25) = 4.74, p = .04, \eta_p^2 = .16$. Finally, the ANOVA on the global performance index of Hits-FAs was characterized by the main effect of congruency at encoding, with better memory performance for items that were congruent than incongruent with the category at encoding, $F(1,25) = 80.19, p < .001, \eta_p^2 = .76$, and a main effect of typicality, with overall better recognition memory performance for atypical than typical items, $F(1,25) = 20.43, p < .001, \eta_p^2 = .45$. The interaction was not significant, $F(1,25) = 0.01, p = .95, \eta_p^2 = .01$ (see Fig. 3).

3.2. Univariate fMRI results

3.2.1. Category verification task

The factorial analysis showed a main effect of congruency such that items that were incongruent with the category (compared to congruent ones) elicited greater activation in the left postcentral gyrus and left middle temporal gyrus as well as in the right precuneus and the right angular gyrus. The main effect of typicality revealed greater activity for the typical than the atypical items in the bilateral angular gyrus, right middle frontal gyrus, medial prefrontal cortex and left precuneus, while the activation was greater for atypical than typical items in the left opercular part of the inferior frontal cortex. The congruency by typicality interaction revealed greater activation in the bilateral thalamus and bilateral precuneus for categorizing typical items compared to atypical items in the congruent condition, with no differences in typicality for the incongruent condition (Table 3 and Figs. 4 and 5).

3.2.2. Recognition memory task

During retrieval, old items relative to new items engaged more activation in the bilateral angular gyrus, left precuneus, bilateral middle temporal gyrus, left temporal pole, medial prefrontal cortex and right postcentral gyrus. In contrast, activation in the left supramarginal gyrus and right superior parietal lobule was greater for new than old items. No region survived the statistical threshold of significance for the typicality

contrast or the interaction between memory status and typicality (Table 3, and Figs. 6 and 7).

3.3. Representational similarity analyses

We conducted a factorial ANOVA on ERS values maps with typicality (typical, atypical) and level (item, set) as factors. Results for the contrast [(typical_item)-(typical_set)>(atypical_item)-(atypical_set)] yielded a significant interaction in the left precuneus, left nucleus accumbens, right lingual gyrus, and right thalamus. This interaction showed that, in these regions, item values were higher than set values for typical items, but not for atypical items, suggesting that the reinstatement of item-specific patterns of brain activity during retrieval was only observed for typical items (Fig. 8A and B). The reverse contrast [(atypical_item)-(atypical_set)>(typical_item)-(typical_set)] did not show any clusters above the significance threshold.

Finally, the same analysis within our ROI in the ATL showed a significant interaction reflecting reinstatement for typical items, but not for atypical ones (Fig. 8C).

4. Discussion

Despite the importance of concept typicality in the organization of semantic memory, and the influence semantics bears on episodic memory, still little is known about how typicality influences episodic memory and what are its neural correlates. Our study examined the neural correlates associated with item typicality during a semantic category verification task and a subsequent episodic recognition task, and investigated the similarity in the patterns of activation associated with the reinstatement of typical and atypical items from encoding to retrieval.

4.1. Semantic typicality effects

Behaviorally, the results of this study show that typical items are categorized better and faster than atypical items, particularly in the congruent condition, i.e. when the item belongs to the presented category, which is in line with previous literature (Kiran et al., 2007). This

Table 2
Proportions of hits and FAs across confidence ratings.

	Confidence 1		Confidence 2		Confidence 3		Confidence 4	
	Typical	Atypical	Typical	Atypical	Typical	Atypical	Typical	Atypical
Hits - congruent	0.01	0.01	0.04	0.04	0.14	0.09	0.57	0.70
Hits - incongruent	0.02	0.01	0.09	0.06	0.16	0.14	0.29	0.42
False alarms	0.02	0.01	0.07	0.03	0.06	0.05	0.03	0.05

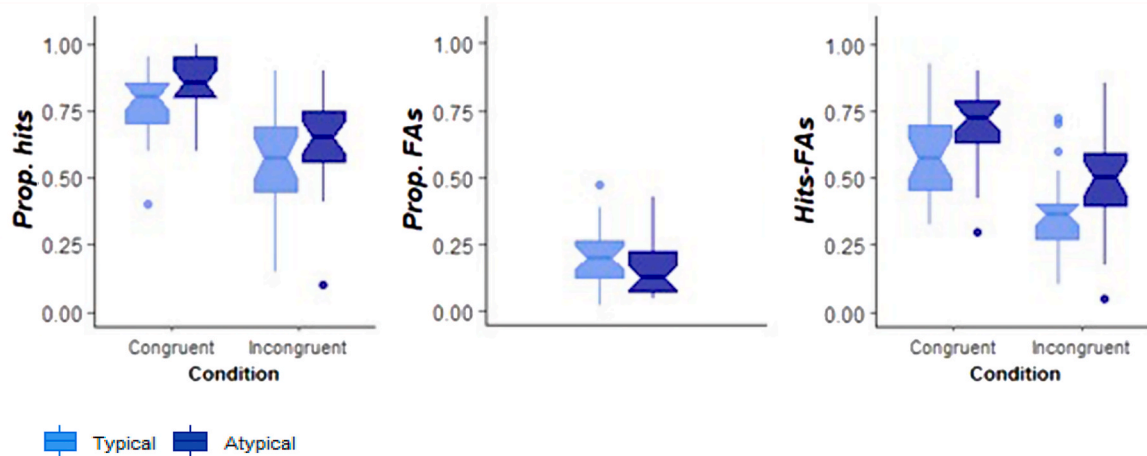


Fig. 3. Proportion of hits (left), false alarms (FAs; middle), and a global index of recognition memory (hits minus FA rates; right) across conditions.

Table 3

Univariate analyses: Peak coordinates of the significant clusters observed in the category verification and recognition memory tasks.

	Region hemisphere	MNI coordinates			F-value	k
		x	y	z		
Category verification task						
Main effect of congruency						
Middle temporal gyrus	L	-50	-50	22	23.08	276
Precuneus	R	6	-54	34	22.49	648
Postcentral gyrus	L	-34	-28	64	21.21	82
Angular gyrus	R	48	-54	24	17.96	138
Main effect of typicality						
Middle frontal gyrus	R	32	38	44	34.94	225
Precuneus	L	-16	-68	22	32.05	2932
Angular gyrus	R	48	-50	18	30.81	1777
Opercular inferior frontal gyrus	L	-44	24	20	25.05	331
Angular gyrus	L	-54	-60	22	19.52	146
Medial prefrontal cortex	R	4	52	-8	17.99	88
Congruency × typicality interaction						
Precuneus	R	10	-46	48	31.46	389
Thalamus	L	-10	-16	16	23.70	128
Precuneus	L	-20	-62	24	20.93	190
Thalamus	R	8	-2	16	20.18	120
Recognition memory						
Main effect of old/new status						
Angular gyrus	L	-38	-72	36	48.69	1540
Precuneus	L	-8	-64	28	44.95	3477
Middle temporal gyrus	R	66	-36	-12	28.24	128
Angular gyrus	R	38	-70	46	25.27	569
Supramarginal gyrus	L	-34	-38	40	24.04	170
Medial prefrontal gyrus	R	6	46	10	21.85	807
Middle temporal gyrus	L	-64	-38	-10	20.35	95
Angular gyrus	R	54	-58	20	20.24	178
Temporal pole	L	-24	64	10	19.29	123
Postcentral gyrus	R	28	-42	44	19.16	168
Superior parietal lobule	R	18	-64	54	18.01	79

indicates that the greater number of features typical items share, compared to atypical items, benefits semantic categorization. These behavioral effects were accompanied by greater activation for typical items in the bilateral AG, right frontal regions and the left precuneus. Activation was instead greater for atypical than typical items in the left

IFG.

Contrary to most studies, we did not find semantic typicality effects in the ATL (Santi et al., 2016; Woollams, 2012; Woollams et al., 2008). Yet, we observed typicality effects in this region during reinstatement of encoding patterns at retrieval, leading us to believe that the ATL was not insensitive to typicality. This result is interpreted more thoroughly below.

Beyond the ATL, a greater activation for atypical than typical items was found in the left IFG, while the opposite was found in the right middle frontal gyrus and the bilateral precuneus, replicating Santi et al.'s (2016). In addition, our study revealed significant recruitment of the right AG during the processing of typical items, corroborating Reilly et al.'s (2019) results of sensitivity to feature distinctiveness in the left IFG, and to feature sharedness in the right AG (though results from Reilly et al. did not survive multiple comparisons correction). The involvement of the IFG in the semantic processing of atypical items supports the hypothesis that this region plays a role in selecting and controlling such information, which is necessary to correctly categorize atypical items due to the lower number of features they share (Badre et al., 2005; Marques, 2007). Besides, distinctive features of an atypical item must be suppressed to decide if it belongs to the category (Santi et al., 2016). In addition, our results are consistent with the idea that the AG is implicated in semantic processing, possibly working as a cross-modal semantic hub, binding the features commonly associated with typical concepts (Bonner et al., 2013; Seghier, 2013).

4.1.1. Episodic old/new effects

Turning to the recognition memory task, correct recognition of old items relative to new ones involved an important network of regions belonging to the core recollection network (i.e., the left PC, bilateral AG, right middle temporal gyrus and medial prefrontal cortex (mPFC)), which is a content-independent network engaged when a retrieval cue elicits recollection and known to mediate the successful retrieval of episodic memories (Rugg and Vilberg, 2013). In addition, more recent fMRI studies have consistently shown that these regions track the strength or precision of recollection based on the richness of memory representations (Sreekumar et al., 2018), through vividness ratings (Richter et al., 2016; St-Laurent et al., 2015; Tibbon et al., 2019), remember judgments (Wang et al., 2016), confidence judgments (Qin et al., 2011), metacognitive decisions (Baird et al., 2013), context-dependent retrieval (Bonnì et al., 2015), as well as mental imagery processes accompanying episodic memory retrieval (Gardini et al., 2006).

Interestingly, recognition of old items recruited the left temporal pole and bilateral middle temporal gyrus, two regions that are considered as part of the ATL (Bonner and Price, 2013), and thus, a key hub in

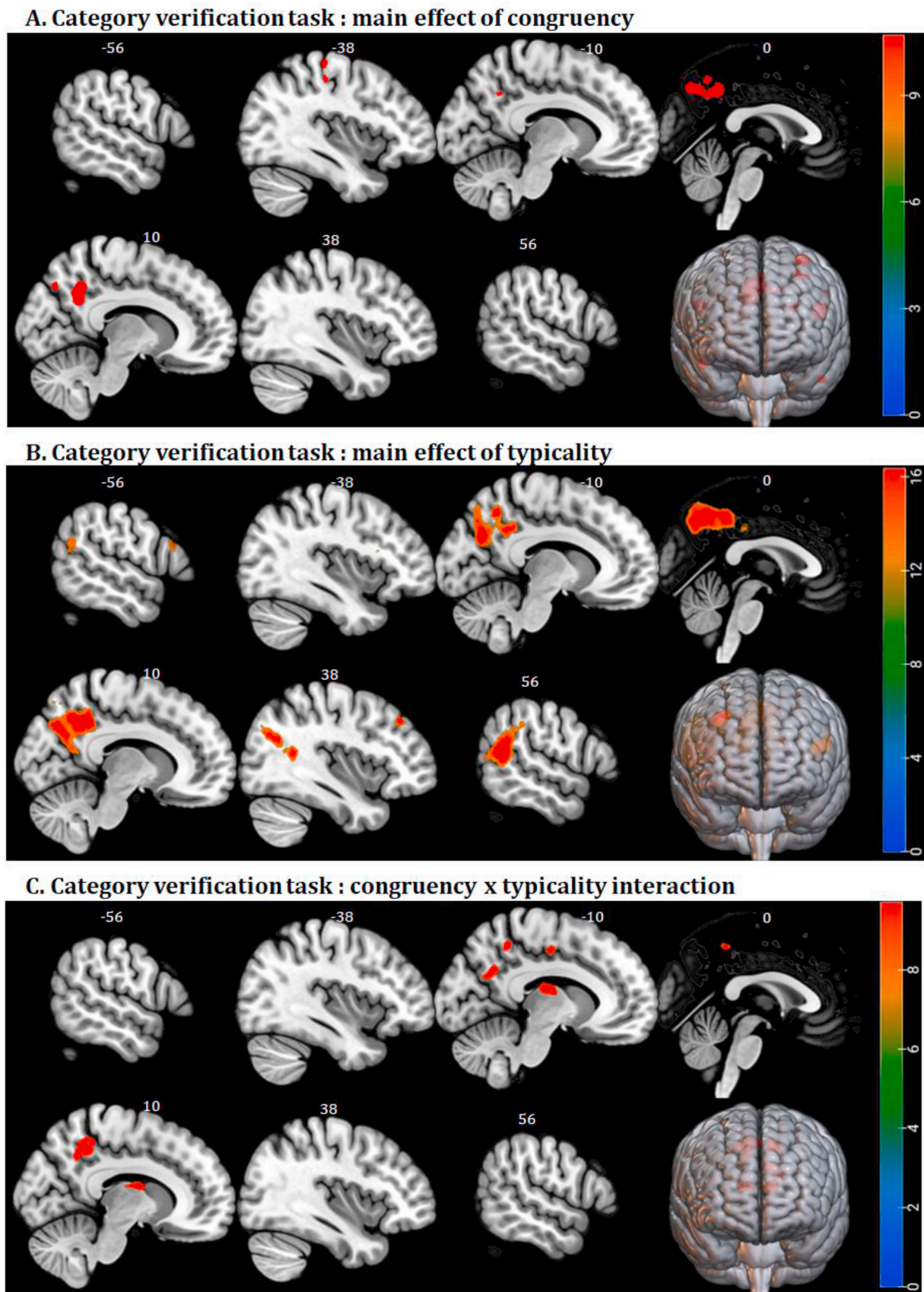


Fig. 4. Significant activation clusters in the category verification task. Heatmap values reflect BOLD signal response.

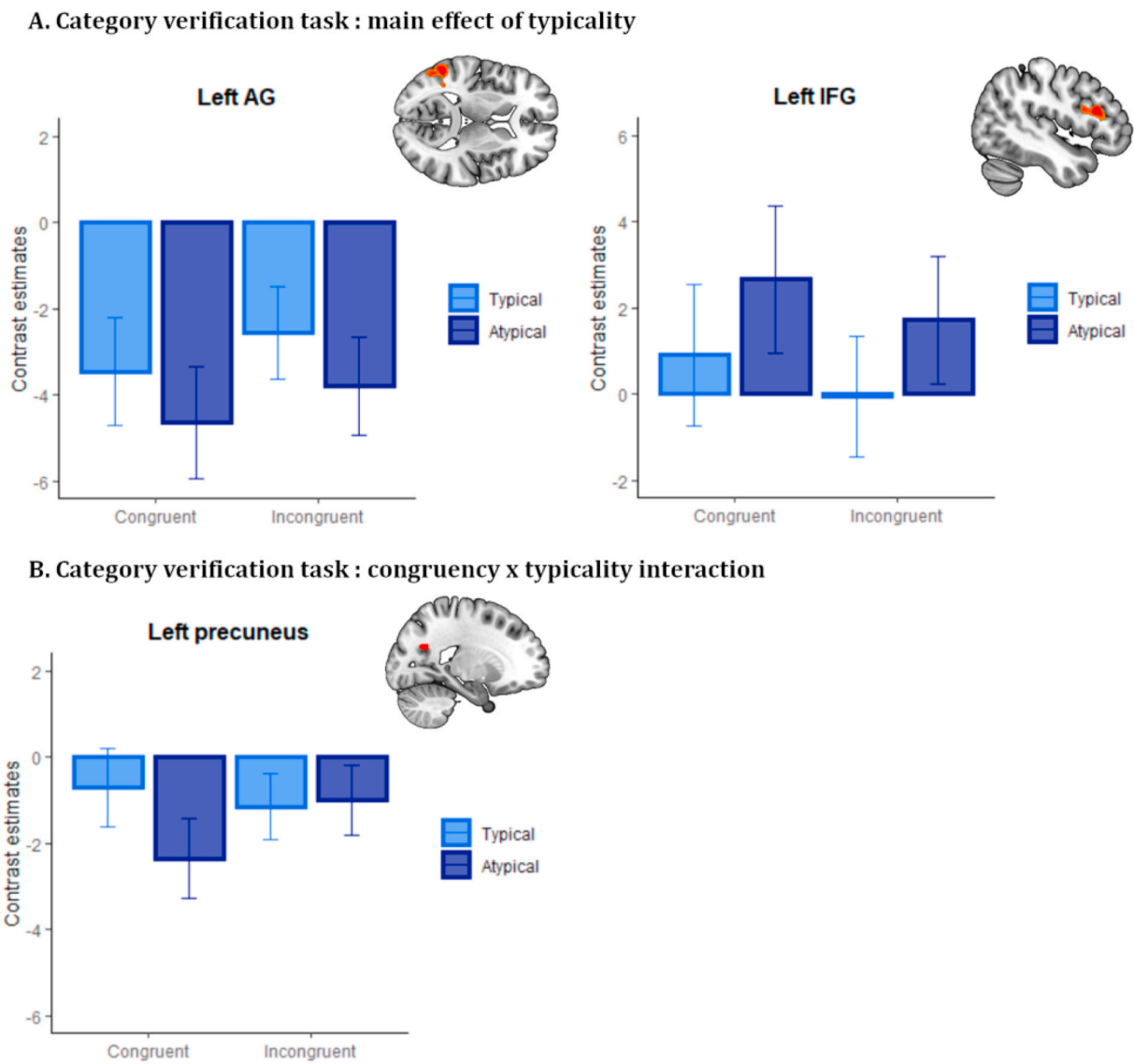


Fig. 5. Contrast estimates in significant clusters of the A) typicality contrast, and B) interaction between typicality and congruency, in the category verification task.

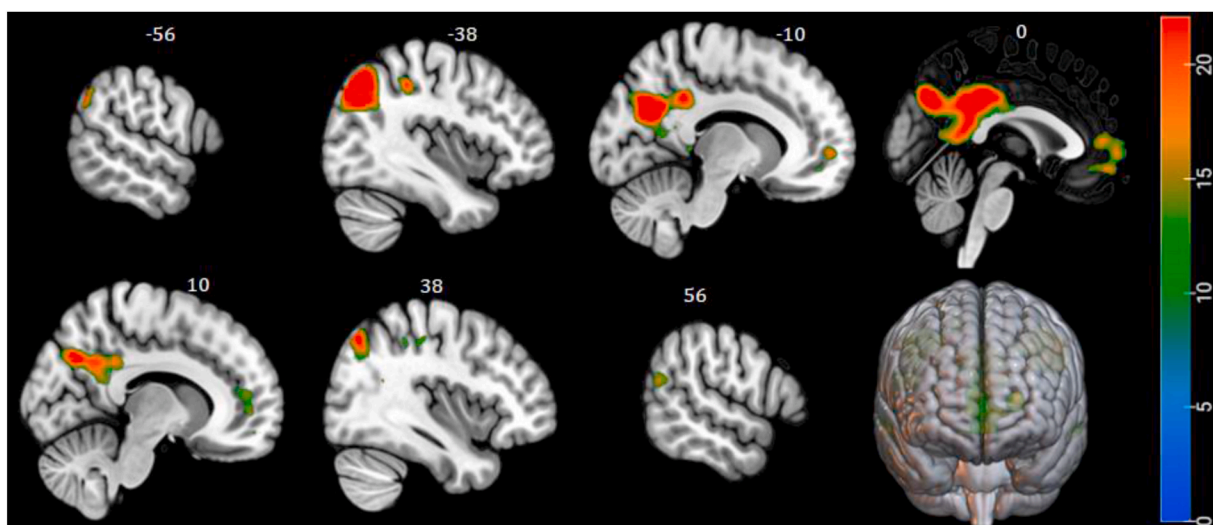


Fig. 6. Clusters showing significant activations in the old/new contrast of the recognition memory task. Heatmap values reflect BOLD signal response.

Recognition memory task: main effect of memory status

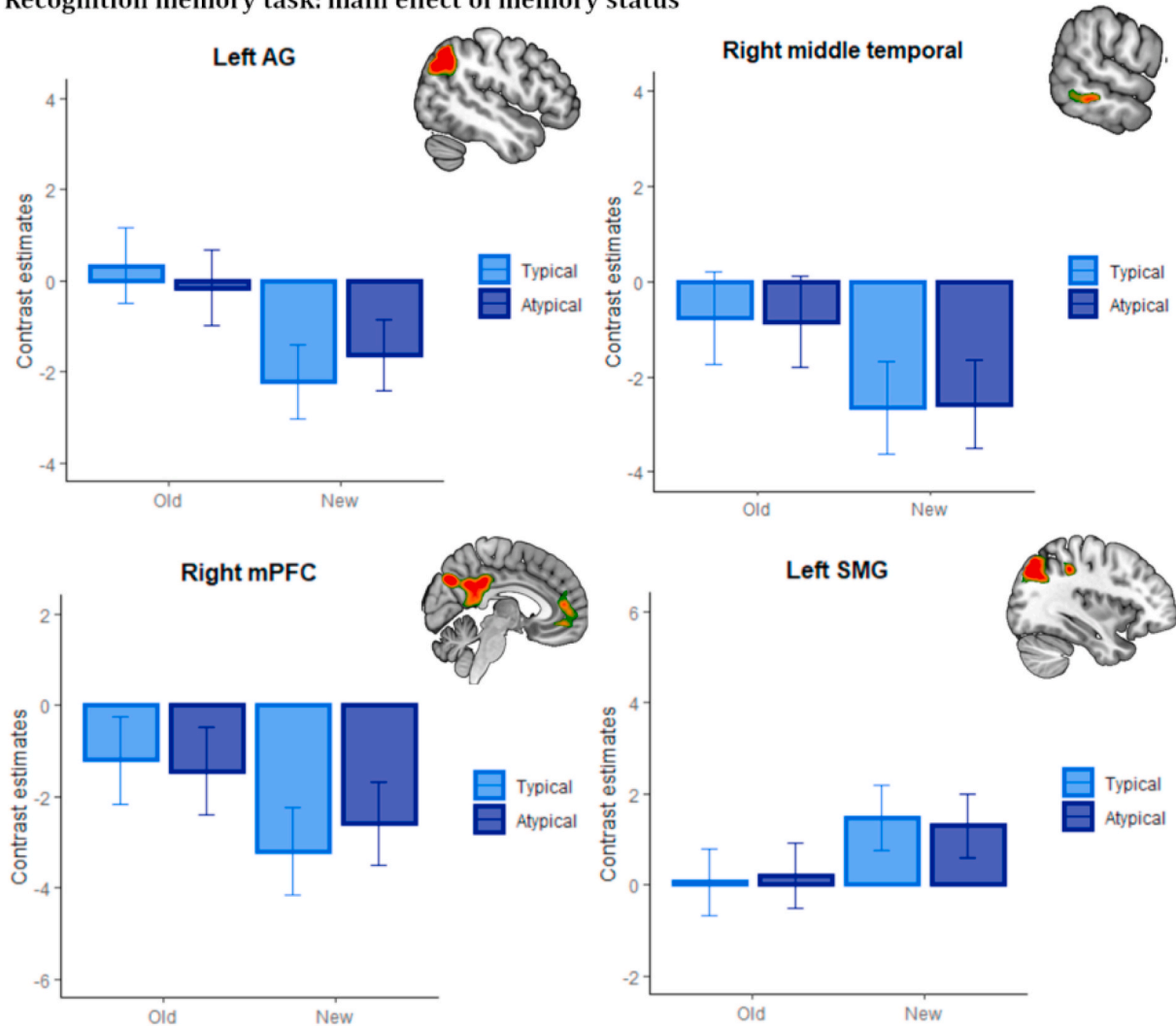


Fig. 7. Contrast estimates in significant clusters of the old/new contrast in the recognition memory task.

the semantic network. These results may suggest that the ATL is involved in the processing and retrieval of object concepts (regardless of their typicality). The PC, AG and mPFC are thought to play a role in post-retrieval monitoring processes, assessing the accuracy in attributing an experience to the past (mPFC) and the strength of recollection (AG), thus possibly contributing to the production of confidence ratings (Baird et al., 2013; Qin et al., 2011; Rugg and Vilberg, 2013; Sreekumar et al., 2018).

4.1.2. Episodic typicality effects

Behaviorally, we found greater recognition accuracy for atypical than typical items, and higher confidence judgments in their correct recognition, which is in line with the existing literature (Alves and Raposo, 2015; Souza et al., 2021). Contrary to the semantic category verification task, this suggests that the higher number of shared features in typical items hampered their recognition, possibly because of the inherent confusability of typical items, i.e., they share more features. Indeed, the distinctiveness of atypical items led to a higher recognition rate (hits), while typical items led to greater false alarm rates, possibly due to their greater confusability. Yet, these behavioral differences were not associated with different patterns of neural activation in the univariate analyses, although they were associated with differences in their reinstatement patterns, as assessed through ERS analyses. Indeed, one advantage of RSA-based analysis is that it treats all items in the design

individually before averaging them, thereby providing finer insights on their relationships and associated patterns of activation, rather than contrasting items grouped by condition as classically done in univariate analysis (Dimsdale-Zucker and Ranganath, 2018).

We found greater reinstatement from encoding to retrieval for typical than atypical items in the left accumbens, left PC, right lingual gyrus and right thalamus. These results favor the idea that typical items which share more features and are so more confusable, require greater reinstatement to reach successful retrieval. Presumably, reinstatement helps to overcome the interference arising from distractors with whom typical items share many features. Interestingly, reactivation of the left PC is in line with the role of this region in both episodic and semantic processing (Binder et al., 2009) and more specifically its function in coding conceptual representations. Notably, Fairhall and Caramazza (2013) and Liuzzi et al. (2020), showed that, in a typicality judgement task, semantically more similar categories also display more similar neural patterns in the PC, which makes it a candidate region for the supramodal representation of the conceptual properties of objects. We extend this effect to retrieval, by showing greater reinstatement of semantic encoding processes for typical items which are conceptually more similar than atypical objects. Yet, here, contrary to previous studies, the PC showed similarity patterns not at the category-level, but at the item-level. So, the role of the PC in reinstating conceptual processing during episodic decisions remains open and needs to be explored

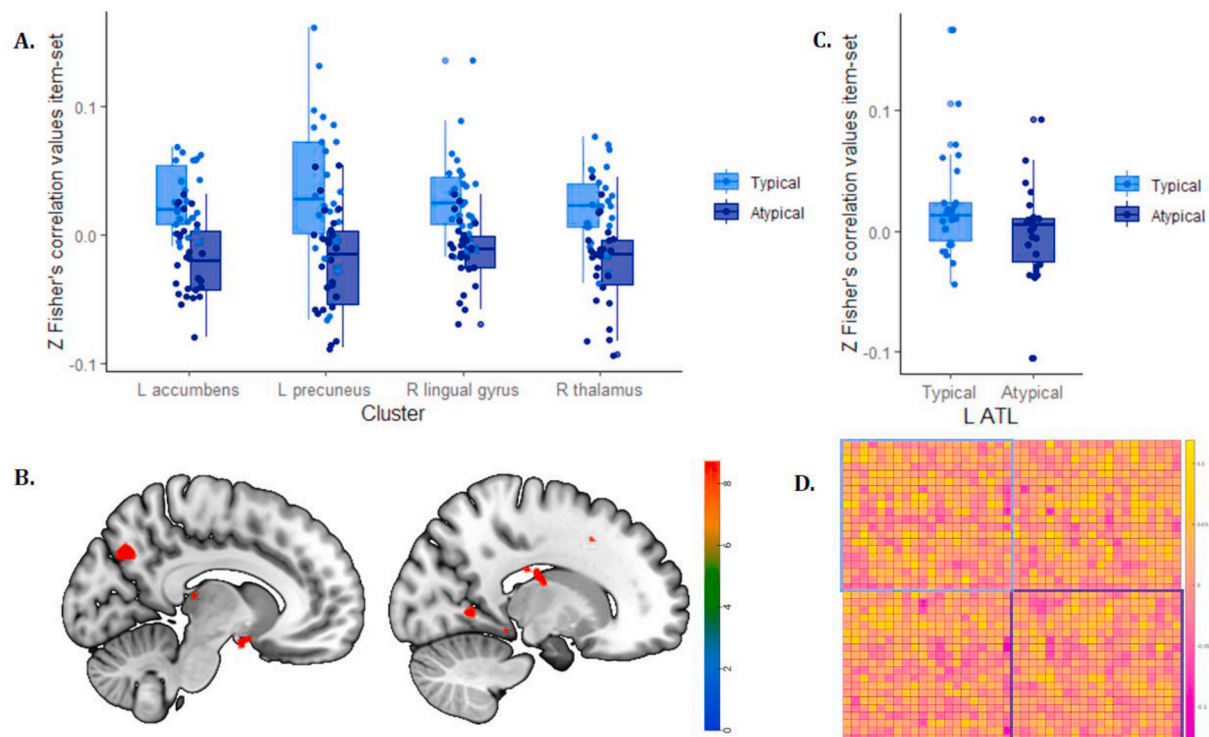


Fig. 8. A. Item-set Fisher's Z correlation values of the clusters showing significant ERS patterns for typical and atypical items in searchlight analyses; B. Illustration of the significant clusters in searchlight analyses (heatmap values reflect BOLD signal response); C. Item-set Fisher's Z correlation values of the significant ERS patterns for typical and atypical items in the ATL ROI analysis; D. Heatmap illustrating Fisher-Transformed Pearson correlations of ERS values in the left precuneus. Typical items are indicated by a light blue rectangle, and atypical items by a dark blue rectangle.

further in future research.

Importantly, our ROI analysis showed evidence for reinstatement in the left ATL, which is thought to be a central hub integrating features into complex representations of objects (Brüett et al., 2020; Bruffaerts et al., 2019; Coutanche and Thompson-Schill, 2015). This result corroborates extensive literature showing links between items similarity, as indexed by the features they share or make them distinctive, and the similarity of activation patterns in the ATL (Bruffaerts et al., 2013; Chen et al., 2016; Clarke, 2020; Clarke and Tyler, 2014; Fairhall and Caramazza, 2013; Liuzzi et al., 2015; Martin et al., 2018). This result seems to be robust across different types of processes, as long as they require fine-grained representations, i.e., from semantic decisions to episodic discrimination like in this task.

4.1.3. Limitations

Reinstatement from encoding to retrieval, however, in our case, also comes with a limitation, which is that the task performed differs, from category verification during encoding, that might require greater processing of shared features, to memory discrimination, which might rely more heavily on distinctive features (cf. semantic control, Ralph et al., 2017). It is thus possible that participants did not reinstate the same processes from encoding to retrieval, and this might have impacted our results through decreased similarity of activations between encoding and retrieval. In the same vein, because the tasks differed from encoding to retrieval, trials from both tasks did not present the same structure (e.g., presence vs. absence of a category cue; presence vs. absence of confidence rating), which might also have diminished ERS. Future studies should explore how the processing demands of the encoding and retrieval tasks (while following an identical trial structure) impact reinstatement, especially for atypical items, for which we were not able to show evidence of reinstatement.

5. Conclusion

To conclude, item typicality influences category verification through differential activations in IFG and AG consistent with prior work. Furthermore, item typicality modulates episodic memory through differential patterns of reinstatement in several regions including the left PC and ATL. Future research is still needed to better understand the role of the left PC in semantic processing and episodic reinstatement of semantic information, as well as to investigate the replicability of these findings across different materials, such as visual items.

CRediT author statement

Ana Raposo: Conceptualization, Methodology, Investigation, Supervision, Writing- Reviewing and Editing; **Emma Delhaye:** Data curation, Formal analysis, Writing- Original draft preparation, Visualization; **Mohamed A. Bahri:** Formal analysis, Software; **Moreno I. Coco:** Funding acquisition, Supervision, Writing- Reviewing and Editing.

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Declaration of competing interest

None.

Data availability

Data will be made available on request.

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