1   Typicality in the brain during semantic and episodic memory decisions

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1 **Abstract**

2 Concept typicality is a key semantic dimension supporting the categorical organization of items based

3 on their features, such that typical items share more features with other members of their category than

4 atypical items, which are more distinctive. Typicality effects manifest in better accuracy and faster

5 response times during categorization tasks, but higher performance for atypical items in episodic

6 memory tasks, due to their distinctiveness. At a neural level, typicality has been linked to the anterior

7 temporal lobe (ATL) and the inferior frontal gyrus (IFG) in semantic decision tasks, but patterns of brain

8 activity during episodic memory tasks remain to be understood. We investigated the neural correlates

9 of typicality in semantic and episodic memory to determine the brain regions associated with semantic

10 typicality and uncover effects arising when items are reinstated during retrieval. In an fMRI study, 26

11 healthy young subjects first performed a category verification task on words representing typical and

12 atypical concepts (encoding), and then completed a recognition memory task (retrieval). In line with

13 previous literature, we observed higher accuracy and faster response times for typical items in the

14 category verification task, while atypical items were better recognized in the episodic memory task.

15 During category verification, univariate analyses revealed a greater involvement of the angular gyrus

16 for typical items and the inferior frontal gyrus for atypical items. During the correct recognition of old

17 items, regions belonging to the core recollection network were activated. We then compared the

18 similarity of the representations from encoding to retrieval (ERS) using Representation Similarity

19 Analyses. Results showed that typical items were reinstated more than atypical ones in several regions

20 including the left precuneus and left anterior temporal lobe (ATL). Our findings confirm the centrality

21 of the ATL in the processing of typicality while extending it to memory retrieval. We also demonstrated

22 that the correct retrieval of typical items requires finer-grained processing, evidenced by greater item-

23 specific reinstatement, which is needed to resolve their confusability with other members of the category

24 due to their higher feature similarity.

25

26 Keywords: episodic memory, semantic memory, fMRI, typicality

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1   **Introduction**

2   Semantic and episodic memory are two declarative long-term memory systems known to interact very

3   closely (Tulving, 1972, 1985). The former holds our semantic knowledge about the world, abstracted

4   away from our experiences (e.g., the meaning of words) and applied to a variety of contexts. The latter

5   instead refers to episodic events personally experienced in the past, which emerges from the binding of

6   information that co-occurred in the specific context where the event took place. Even though the

7   independence of these two systems is supported by neuroimaging and clinical evidence (Tulving, 1972,

8   1985), they also demonstrate an interplay, such that semantic processing may, for example, enhance

9   episodic retrieval (e.g., levels of processing and semantic congruency effects, Bartlett, 1932; Craik &

10   Lockhart, 1972) or, instead, hinder episodic remembering (e.g., giving rise to false memories; see

11   Greenberg & Verfaellie, 2010 for review). Recent research has questioned the idea of a clear separation

12   between episodic and semantic systems, as they seem to be supported by at least partially overlapping

13   brain networks and common retrieval processes (Greenberg & Verfaellie, 2010; Irish & Vatansever,

14   2020; Renoult et al., 2019).

15   One of the most integrative theoretical accounts of semantic memory, the Hub-and-Spoke model, holds

16   that semantic categories arise from intrinsic regularities among conceptual features of objects.

17   According to this model, the anterior temporal lobe (ATL), which includes the temporal gyri, temporal

18   pole, rhinal cortices, fusiform and parahippocampal gyri (Bonner & Price, 2013), works as a semantic

19   hub, which amodally integrates conceptual information and forms abstractions or generalizations across

20   categories (Patterson et al., 2007; Ralph Lambon et al., 2017). Yet, it remains unclear how the natural

21   variability in the conceptual features of items of the same category is represented by the human brain,

22   with some authors relating it to their typicality (Santi et al., 2016; Woollams, 2012; Woollams et al.,

23   2008). Indeed, a key property of concepts is their graded category membership, according to which some

24   members are more typical, or a better exemplar of the category than others (Rosch & Mervis, 1975).

25   Within a given category (e.g., bird), a typical item (e.g., sparrow) shares many features with the other

26   members of its category while, conversely, an atypical item (e.g., penguin) is characterized by more

27   idiosyncratic features, making atypical items more distinctive within their category. Hence, according

28   to some authors, typicality reflects the conceptual structure as expressed by the co-occurrence of features

29   between concepts within a given category (Raposo et al., 2012).

30   Behaviorally, typical items are systematically associated with faster response times and lower error rates

31   than atypical items in naming (Holmes & Ellis, 2006) and category verification tasks (Kiran et al., 2007).

32   However, at a neural level, results are more inconsistent, which may be partly due to the different tasks

33   used (i.e., naming, categorization, feature verification) or the stimuli adopted (words vs. pictures; e.g.,

34   see Davis & Poldrack, 2014; Iordan et al., 2016; Li et al., 2021). On one hand, studies on patients with

35   semantic dementia (SD), presenting with ATL atrophy (Woollams et al., 2008), and with healthy

controls following Transcranial Magnetic Simulation (TMS) on the ATL (Woollams, 2012), showed that disruption of the ATL leads to impairments in naming tasks for more atypical concepts, and an fMRI study with healthy participants showed 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) have shown that, in the ATL region, the semantic similarity between concepts (as measured by feature norms, indexing their shared and distinctive features) matches similarity between voxel patterns elicited by objects processed semantically (Borghesani et al., 2016; Bruffaerts et al., 2013; Chen et al., 2016; Clarke, 2020; Clarke & Tyler, 2014; Fairhall & 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 as unique complex entities according to the integration of their constituting features, both shared and distinctive ones (Bruett et al., 2020; Bruffaerts et al., 2019; Coutanche & 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 & 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 for integration 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 & 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 & 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 Höltje 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; Woollams et al., 2012). 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 and results in greater item-unique effects. 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.

Methods

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.

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) in an independent group

of participants who judged how typical an exemplar is for a given category on a 7-point scale (1=very atypical to 7=very typical).

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 the number of letters (all ps > .29; see Table 1). 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 Figure 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 Figure 1 for an example of the design of the tasks.
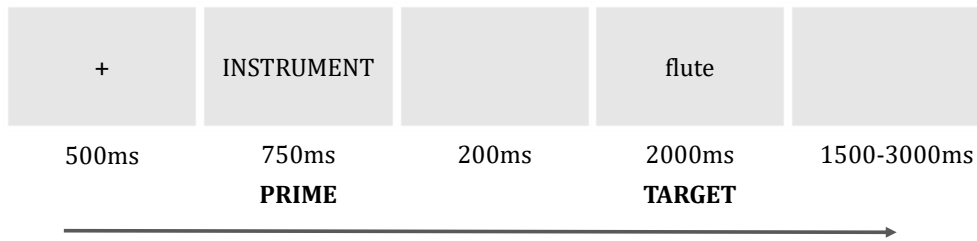
Table 1. *Descriptive statistics (mean, and SD in brackets) of the stimuli characteristics*

		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

+	INSTRUMENT		flute	
500ms	750ms	200ms	2000ms	1500-3000ms
	PRIME		**TARGET**	

Retrieval (scanned) – old/new recognition memory task

+	flute		1 2 3 4	
500ms	2500ms	200ms	2000ms	2000-3500ms
	PROBE		**CONFIDENCE JUDGEMENT**	

Figure 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

MRI data acquisition and preprocessing

Scanning was conducted at Sociedade Portuguesa de Ressonância Magnética on a 3T Philips MR system (Philips Medical Systems, Best, NL) using a standard head coil. Functional data were acquired by using an echo-planar sequence (TR=2000ms, TE=23ms, FA=90°, FOV=230×230 mm, 34 bottom-up interleaved slices parallel to the AC-PC line, with 1.8 x 1.8 x 3.5 mm voxels size, matrix size=116x115). 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 normalisation).

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 2015b, Mathworks 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 x 2 x 2 mm. The normalization parameters were then applied to the preprocessed functionals. Normalized functional data were then spatially smoothed with an isotropic Gaussian kernel of 8 mm FWHM.

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.

fMRI data analyses

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 sec). 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 sec). 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: $M=.56$, SD=0.18; incongruent atypical: $M=.64$, 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, and the cluster-level threshold of 78 contiguous (resampled) voxels (k), to correct for multiple comparisons, at $p<.05$, as determined by Monte Carlo simulations (N iterations 10 000) using the current study's imaging and analysis parameters as recommended by Slotnick et al. (2003).

Multivariate analyses

RSA was used to examine the neural similarity of typical and atypical items from encoding to retrieval (Encoding-Retrieval Similarity, ERS) across participants (Kriegeskorte et al., 2008). The unsmoothed preprocessed fMRI images were used for these analyses. A beta value was generated for each trial of encoding and retrieval. Trials were modelled as 0 s-duration events (see Folville et al., 2020; Wing et al., 2015, for a similar approach), along with regressors corresponding to realignment as nuisance parameters to model movement-related variance. The CoSMoMVPA toolbox (Oosterhof et al., 2016) was then used to perform RSA analyses using the resulting betas. To examine neural similarity across participants, a searchlight procedure was used (Kriegeskorte et al., 2008).

For each trial, we computed ERS at the item level (corresponding to the similarity of patterns of brain activity between the encoding and retrieval of a given item) and the set level (i.e., the comparison of the patterns of brain activity associated with the retrieval of a given item with patterns of brain activity associated with the encoding of the remaining items from the same condition – typical or atypical). The set level measures the general reactivation of concept processing, while the item level measures the specific reactivation of a given concept. Thus, any difference observed between the item and the set levels indicates that cognitive processes specific to a given concept were reactivated during retrieval (see Figure 8D for an illustration of the ERS matrix).

For both the item and set levels, we applied a searchlight to the betas (Kriegeskorte et al., 2008) with a vectorized 3 x 3 x 3 voxel cube, and Fisher-Transformed Pearson correlations were used to measure ERS. In the item level ERS analysis, the correlation was computed between encoding and retrieval for each item (e.g., flute x flute). In the set–level ERS analysis, for a given item, the retrieval of this item was correlated with the encoding of the remaining items (e.g., flute x piano, flute x sparrow, flute x coat, etc.) and the correlations were averaged. Thus, for each item and each voxel, we obtained a correlation value for the item and the set level. Then, 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 ERS 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 10mm-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 & Thompson-Schill, 2015). The same 2 typicality (typical, atypical) by 2 levels (item, set) factorial ANOVA was run on ERS maps within this ROI.

Results

***Behavioral results***

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, $F(1,25)=31.79$, $p<.001$, $\eta^2_p=.56$, with better performance for incongruent than congruent targets. There was also a main effect of typicality, $F(1,25)=43.76$, $p<.001$, $\eta^2_p=.64$, with more accurate categorization of typical than atypical items. The congruency x typicality interaction was also significant, $F(1,25)=64.43$, $p<.001$, $\eta^2_p=.72$, 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 Figure 2).

Regarding response times, we found a main effect of typicality, $F(1,25)=57.29$, $p<.001$, $\eta^2_p=.68$, with typical items leading to faster responses than atypical items. There was no main effect of congruency,

1 $F_{(1,25)}=0.83$, $p=.37$, $\eta^2_p=.03$, but there was a significant interaction between congruency and typicality,

2 $F_{(1,25)}=25.00$, $p<.001$, $\eta^2_p=.48$, showing no difference in response time between typical and atypical

3 items in the incongruent condition ($p=.41$), while typical items led to faster response times than atypical

4 items in the congruent condition ($p<.001$).
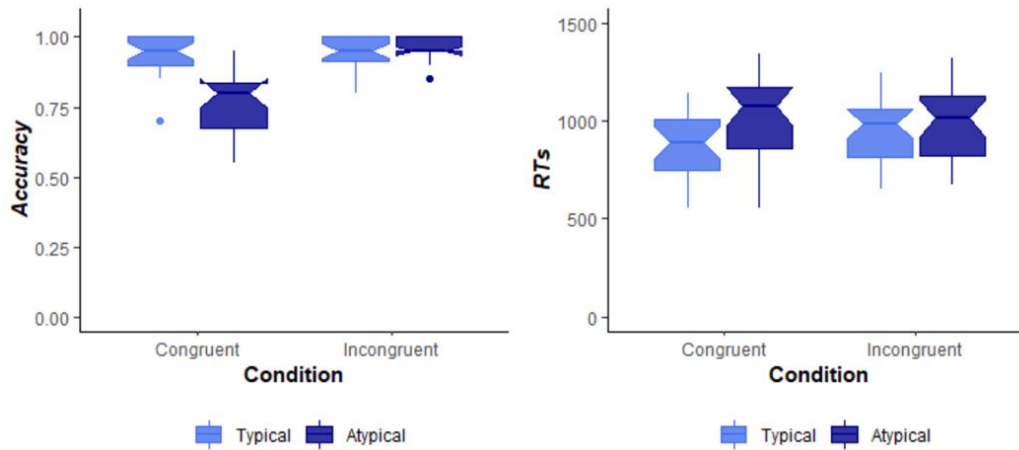
6 Figure 2. Accuracy (left) and response times for correct trials (in ms, right) in the category verification task for

7 congruent and incongruent trials across conditions of typicality

8 *Recognition memory task*

9 The ANOVA on hit rates with congruency (congruent, incongruent) and typicality (typical, atypical) as

10 within-subject variables revealed that congruency at encoding impacted subsequent recognition, with

11 higher hit rates for items that were congruent with the presented category than incongruent ones,

12 $F_{(1,25)}=80.19$, $p<.001$, $\eta^2_p=.76$. There was also a main effect of typicality, with higher hit rates for

13 atypical than typical items, $F_{(1,25)}=11.84$, $p=.002$, $\eta^2_p=.32$. The interaction between congruency at

14 encoding and typicality was not significant, $F_{(1,25)}=0.01$, $p=.95$, $\eta^2_p=.01$. The same analysis on high

15 confidence responses only (level 4 of confidence) revealed the same pattern of results, with the main

16 effect of congruency showing more hits for congruent than incongruent items, $F_{(1,25)}=171.45$, $p<.001$,

17 $\eta^2_p=.87$, a main effect of typicality with more high confidence hits for atypical than typical items,

18 $F_{(1,25)}=48.81$, $p<.001$, $\eta^2_p=.66$, and no interaction between congruency and typicality, $F_{(1,25)}=0.01$,

19 $p=.95$, $\eta^2_p=.01$ (Table 2). There was a significantly greater proportion of false alarms in the typical than

20 atypical condition, $F_{(1,25)}=4.74$, $p=.04$, $\eta^2_p=.16$. Finally, the ANOVA on the global performance index

21 of Hits-FAs was characterized by the main effect of congruency at encoding, with better memory

22 performance for items that were congruent than incongruent with the category at encoding,

23 $F_{(1,25)}=80.19$, $p<.001$, $\eta^2_p=.76$, and a main effect of typicality, with overall better recognition memory

24 performance for atypical than typical items, $F_{(1,25)}=20.43$, $p<.001$, $\eta^2_p=.45$. The interaction was not

25 significant, $F_{(1,25)}=0.01$, $p=.95$, $\eta^2_p=.01$ (see Figure 3).
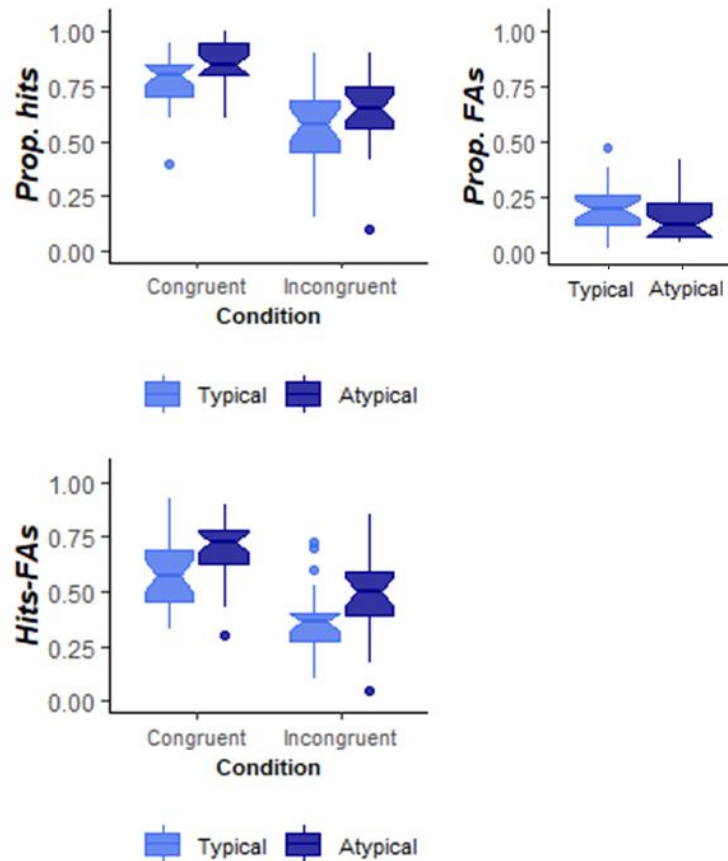
Figure 3. Proportion of hits (upper left), false alarms (FAs; right), and a global index of recognition memory (hits minus FA rates; lower left) across conditions

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

Univariate fMRI results

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 Figures 4 and 5).

A. Category verification task : main effect of congruency
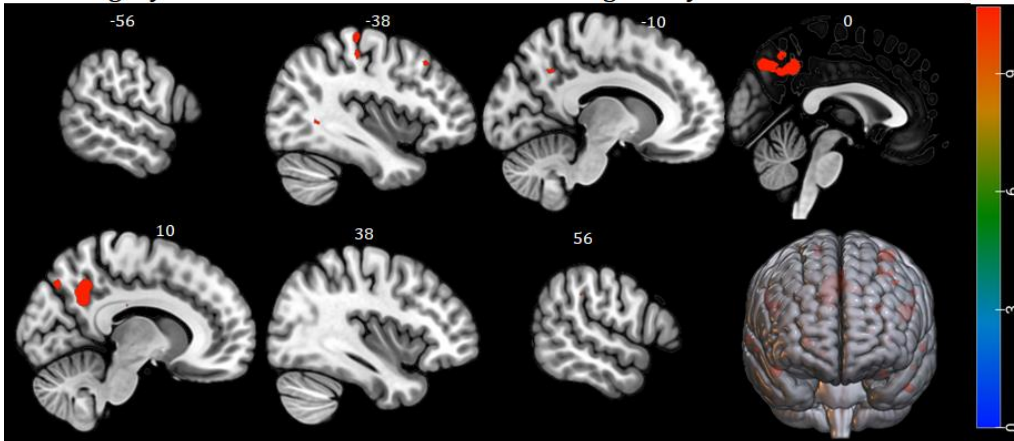
B. Category verification task : main effect of typicality
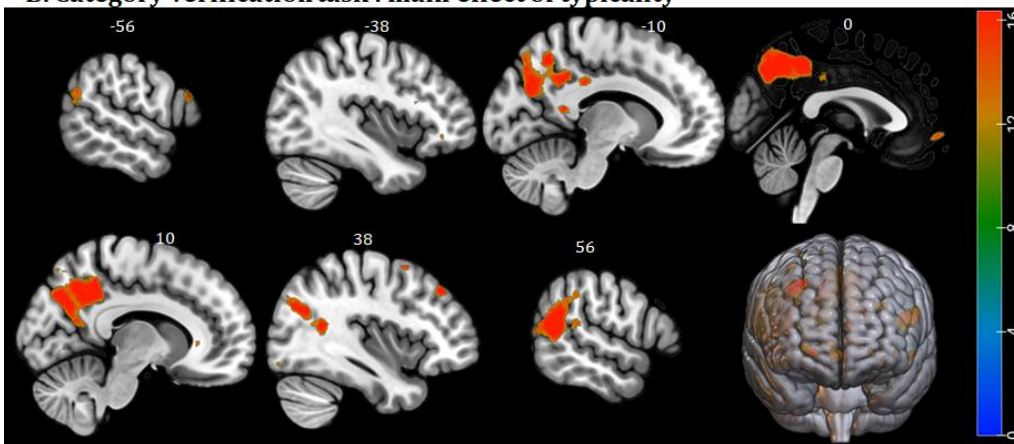
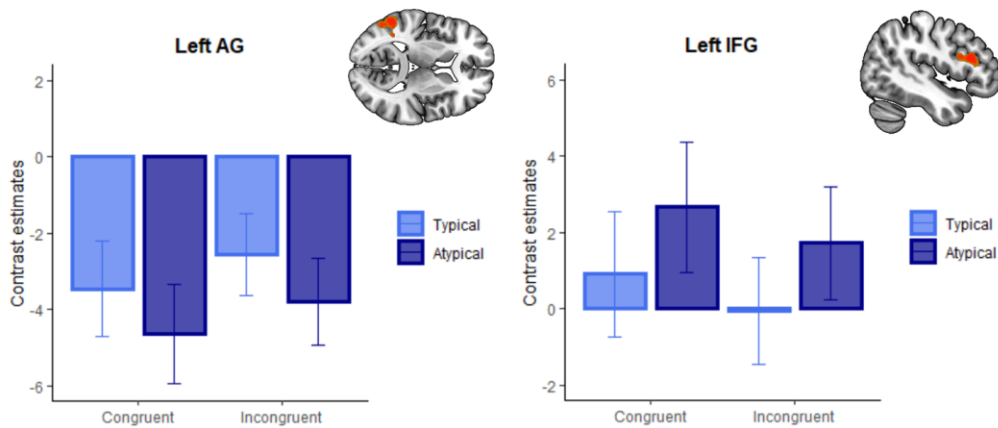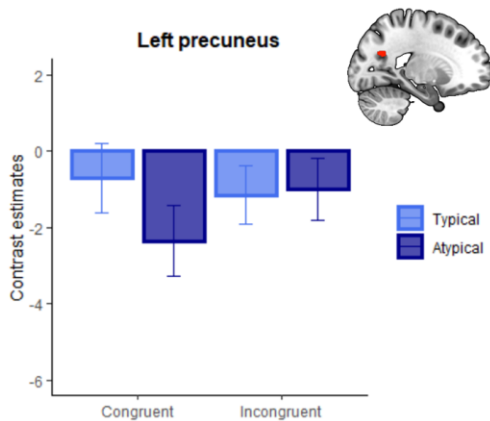**C. Category verification task : congruency x typicality interaction**

Figure 4. Significant activation clusters in the category verification task

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

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 Figures 6 and 7).

|	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 x 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

1

2   Table 3. Univariate analyses: Peak coordinates of the significant clusters observed in the category verification

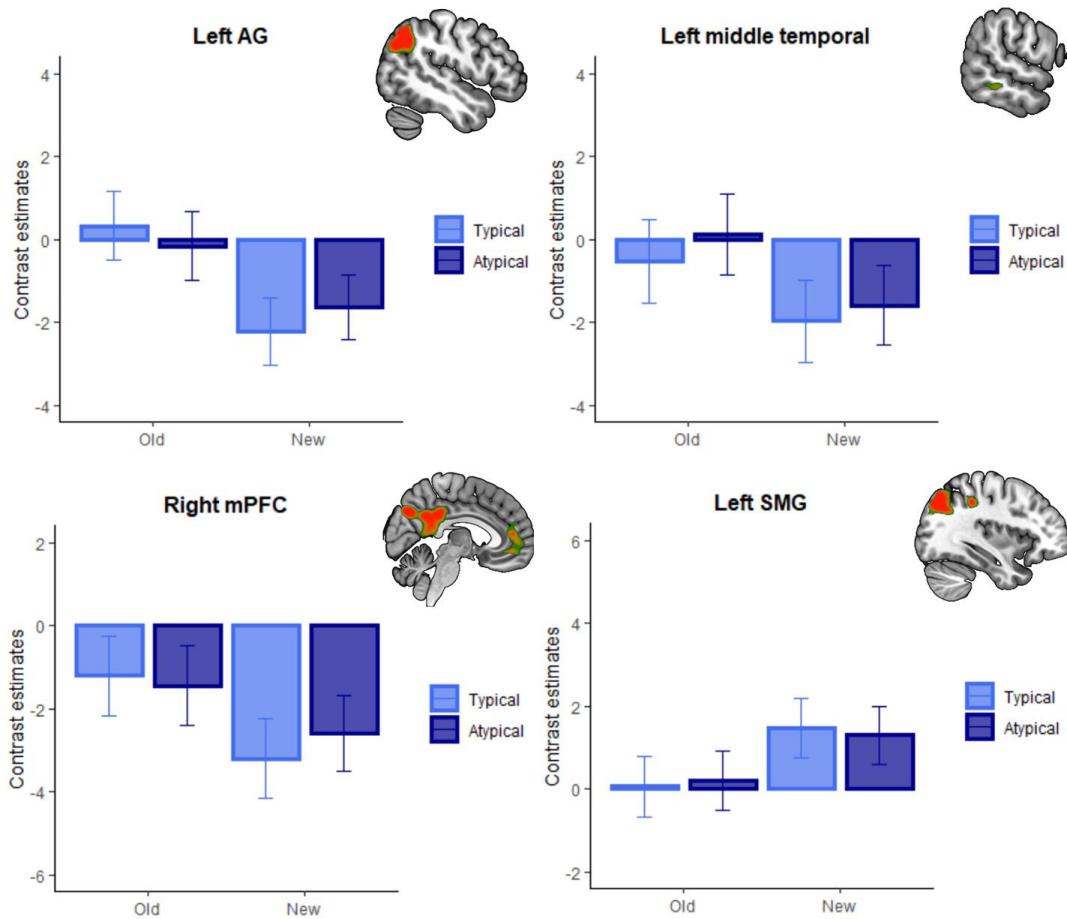3   and recognition memory tasks
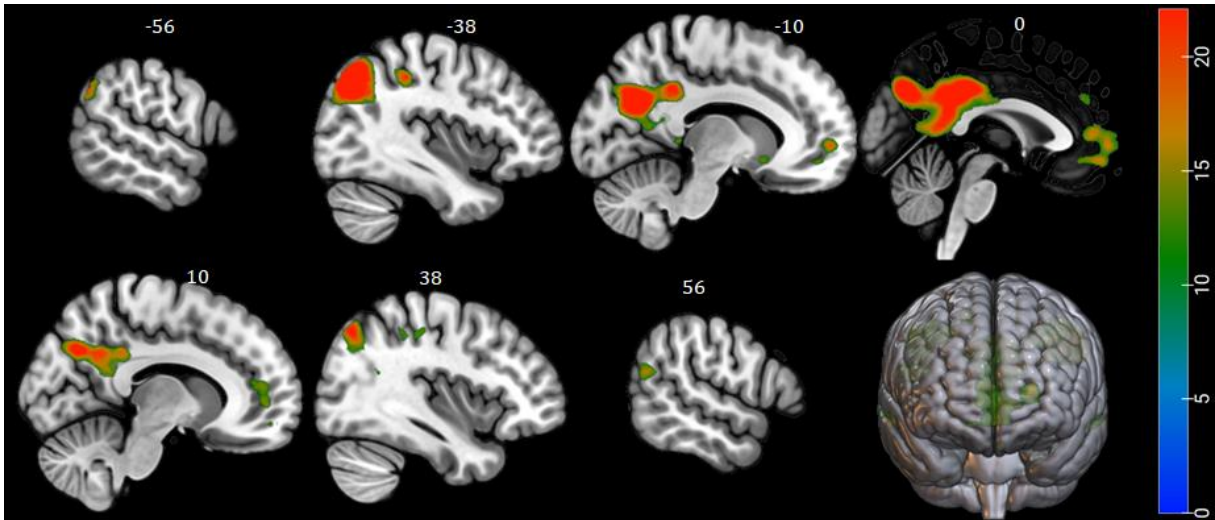
Figure 6. Clusters showing significant activations in the old/new contrast of the recognition memory task

Recognition memory task: main effect of memory status

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

Representational Similarity Analyses

We conducted a factorial ANOVA on ERS values maps with typicality (typical, atypical) and level (item, set) as factors. Results 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 (Figure 8A and 8B). The reverse contrast 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 (Figure 8C).
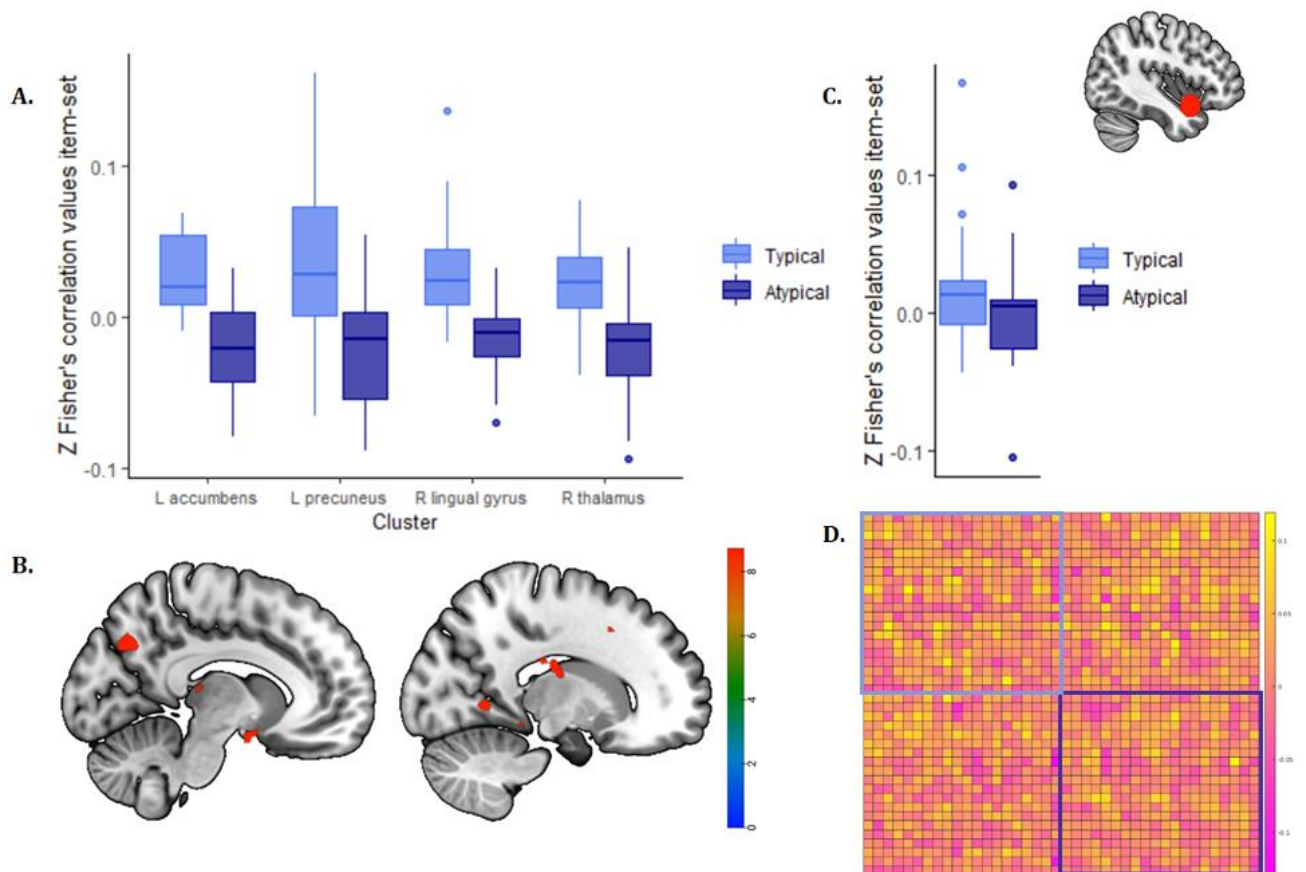
Figure 8. A. Item-set Fisher's Z correlation values of the clusters showing significant ERS patterns for typical and atypical items in searchlight analyses; B. Illustration of the significant clusters in searchlight analyses; C. Item-set Fisher's Z correlation values of the significant ERS patterns for typical and atypical items in the ATL

1   ROI analysis; D. Heatmap illustrating Fisher-Transformed Pearson correlations of ERS values in the left

2   precuneus. Typical items are indicated by a light blue rectangle, and atypical items by a dark blue rectangle

3

4

1 **Discussion**

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

8 *Semantic typicality effects*

9 Behaviorally, the results of this study are in line with the existing literature by showing that typical items
10 are categorized better and faster than atypical items, particularly in the congruent condition, i.e. when
11 the item belongs to the presented category (Kiran et al., 2007). This indicates that the greater number of
12 features typical items share, compared to atypical items, benefits semantic categorization. These
13 behavioral effects were accompanied by greater activation for typical items in the bilateral AG, right
14 frontal regions and the left precuneus. Activation was instead greater for atypical than typical items in
15 the left IFG.

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

20 Beyond the ATL, our study replicated Santi et al.'s (2016) results of greater activation for atypical items
21 in the left IFG, as well as greater activation for typical items in the right middle frontal gyrus and the
22 bilateral precuneus. In addition, our study revealed significant recruitment of the right AG during the
23 processing of typical items, corroborating Reilly et al.'s (2019) results of sensitivity to feature
24 distinctiveness in the left IFG, and to feature sharedness in the right AG (though results from Reilly et
25 al. did not survive multiple comparisons correction). The involvement of the IFG in the semantic
26 processing of atypical items supports the hypothesis that this region plays a role in semantic control and
27 semantic selection (Badre et al., 2005; Marques, 2007). Specifically, greater semantic control is
28 necessary to correctly categorize atypical items due to the lower number of features they share. Besides,
29 distinctive features of an atypical item must be suppressed to decide if it belongs to the category (Santi
30 et al., 2016). In addition, our results are consistent with the idea that the AG is implicated in semantic
31 processing, possibly working as a cross-modal semantic hub, binding the features commonly associated
32 with typical concepts (Bonner et al., 2013; Seghier, 2013).

33 *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, 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 & 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; Tibon 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 & Price, 2013), and thus, a key hub in 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 & Vilberg, 2013; Sreekumar et al., 2018).

Episodic typicality effects

Behaviorally, in line with the existing literature, we found greater recognition accuracy for atypical than typical items, and higher confidence judgments in their correct recognition (Alves & 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 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, 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 & 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 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 (Bruett et al., 2020; Bruffaerts et al., 2019; Coutanche & 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 & Tyler, 2014; Fairhall & Caramazza, 2013; Liuzzi et al., 2015; Martin et al., 2018). Importantly, 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.

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.

8

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