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Neural correlates of concept typicality and category membership

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**Mestrado em Ciência Cognitiva**

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2022

“No one remembers your name  
When you're strange.”

- The Doors (1967)

The Doors. (1967). People are strange. On Strange Days. Elektra.

## Agradecimentos

Gostaria de agradecer, primeiramente, à Professora Ana Raposo, pela oportunidade de me envolver nesta área fascinante que junta a psicologia cognitiva com a neurociência, e ao Professor Alexandre Andrade, por ter aceitado orientar um aluno sem nunca se ter anteriormente cruzado com ele. Agradeço a ambos pelo incentivo, partilha de conhecimento, dedicação e tempo despendido na orientação deste trabalho e no meu desenvolvimento pessoal e académico.

Agradeço à minha tutora de mestrado, a Professora Ana Sebastião, pelas várias conversas e oportunidades que me permitiram conhecer e desenvolver o meu interesse nas neurociências.

Agradeço à minha família, especialmente aos meus pais, por todo o seu amor, esforço e disponibilidade aos longos dos anos, pois sem estes não seria possível a realização deste trabalho. Agradeço pelo apoio que sempre me deram em todas as minhas escolhas e por tudo o que fazem por mim.

Agradeço à Beatriz por todo o seu amor, companhia e ajuda em todos os momentos. Estendo este agradecimento à sua família por todo o seu apoio, são para mim família.

Agradeço aos meus amigos e colegas, pois o longo percurso académico necessita de ajuda e amizade para que chegue a bom porto.

Por fim, agradeço à Professora Iolanda Custódio (ESMTG), à Professora Joana Santos (UALG), à Professora Adelinda Candeias e Professor Edgar Galindo (UÉvora), e à Professora Andreia Sofia Teixeira (ULisboa) por terem sempre acreditado em mim e por me motivarem a ser melhor.

## Resumo

A tipicidade é uma dimensão chave no processamento de conceitos e refere-se ao grau em que um item é representativo da sua categoria. Itens típicos são processados mais facilmente em tarefas de categorização e de nomeação do que itens atípicos. O presente estudo tem como objetivo investigar as bases neuronais da categorização dos objetos e as regiões cerebrais envolvidas no processamento da tipicidade dos objetos. Estudos prévios centraram-se sobretudo na região do lobo temporal anterior e têm fornecido resultados contraditórios entre si. No presente estudo de fMRI, 26 jovens adultos realizaram uma tarefa de categorização, tendo sido manipulada a pertença à categoria e a tipicidade dos conceitos. Os resultados comportamentais e neuronais revelaram um efeito de interação. Objetos típicos foram categorizados mais rápida e acertadamente do que objetos atípicos, mas apenas quando pertenciam à categoria apresentada. A nível neuronal, verificou-se que quando os itens pertenciam à categoria, objetos típicos recrutaram o precuneus esquerdo associado à decisão com base na semelhança, enquanto os objetos atípicos elicitarão maior ativação no lobo frontal inferior esquerdo, que tem sido associado ao controlo semântico. Os resultados confirmam o papel central da tipicidade no processamento semântico e em particular na categorização e informam sobre as bases neuronais da variabilidade intra-categorial.

Palavras-chave: Processamento semântico; Categorização; Tipicidade; fMRI;

## Abstract

Typicality is a key dimension in concept processing and refers to the extent to which an item is representative of its category. Typical items are processed more easily in categorization and naming tasks than atypical items. The present study aims to investigate the neural basis of object categorization and the brain regions involved in processing item typicality. Previous studies have mainly focused on the anterior temporal lobe region and have provided results that are contradictory to each other. In the present fMRI study, 26 young adults performed a categorization task, and category membership and concept typicality were manipulated. Behavioural and neuronal results revealed an interaction effect. Typical items were categorized more quickly and correctly than atypical objects, but only when they belonged to the shown category. At the neuronal level, it was found that when items belonged to the category, typical items recruited the left precuneus associated with similarity-based decision making, whereas atypical items elicited greater activation in the left inferior frontal lobe, which has been associated with semantic control. The results confirm the central role of typicality in semantic processing and in particular categorisation and inform about the neural basis of intra-category variability.

Keywords: Semantic processing; Categorisation; Typicality; fMRI.

## Resumo Alargado

A memória semântica corresponde ao conhecimento geral sobre o mundo, incluindo factos, ideias, normas sociais e conceitos (Tulving, 1983). Um processo fundamental na compreensão e utilização de informação conceptual é a categorização, que permite a organização do conhecimento adquirido e o estabelecimento de relações entre conceitos, facilitando assim a aprendizagem de conceitos novos (Grossman et al., 2002). A tipicidade é uma característica fundamental dos conceitos que influencia a categorização. Refere-se ao grau em que um item é representativo da sua categoria, existindo membros mais representativos de uma categoria do que outros (Rosch & Mervis, 1975; Woollams, 2012). Assim, para uma dada categoria (ex.: mamífero), um item típico (cão) partilha várias características com membros da categoria e poucas características com membros não pertencentes. Por oposição, um item atípico (morcego) partilha mais características com membros não pertencentes e menos com membros da categoria (Woollams, 2012).

O efeito de tipicidade na categorização tem sido vastamente demonstrado na literatura científica. Na população saudável, itens típicos são categorizados com maior rapidez e precisão do que os itens atípicos (Rosch, 1975). Estudos com pacientes com demência semântica, uma doença neurodegenerativa caracterizada pela atrofia e o hipometabolismo dos lobos temporais anteriores (LTA), têm fornecido dados relevantes, já que estes pacientes apresentam maior exatidão na nomeação de objetos típicos do que atípicos (Woollams et al., 2008). Em tarefas de desenho, estes pacientes tendem a adicionar características erróneas com o propósito de tornar os objetos mais “típicos” e a omitir características distintivas e, em tarefas de categorização, tendem a rejeitar objetos atípicos e a categorizar erradamente objetos “pseudo-típicos” (Bozeat et al., 2003;

Mayberry et al., 2011). Um estudo de estimulação magnética transcraniana, em que foi provocada uma “lesão temporária” no LTA em adultos saudáveis, confirmou a maior dificuldade em categorizar objetos atípicos do que típicos (Woollams, 2012).

Em complemento, estudos de ressonância magnética funcional têm procurado examinar as funções de outras regiões cerebrais além do LTA. Santi et al. (2016) mostraram que a categorização de itens típicos envolve o lobo parietal inferior direito e áreas posteriores temporais, regiões que estão associadas ao processamento de semelhanças e à avaliação de protótipos (Grossman et al., 2002). Já a categorização de itens atípicos envolve o LTA esquerdo responsável pela integração de características semânticas distintivas (Woollams, 2012) bem como o córtex frontal inferior bilateral, ligado à função de controlo semântico (Novick et al., 2005). Noutro estudo, Liu et al. (2013) investigaram os correlatos neurais do processamento de objetos que pertencem ou não à categoria, e de objetos típicos e atípicos, em participantes nativos de mandarim e inglês. Para ambos os grupos, houve maior ativação no córtex frontal, lobos parietais inferiores bilaterais e lobos temporais médio e inferior esquerdo para objetos que não pertencem à categoria. Ademais, para falantes de inglês, os objetos atípicos evocaram maior ativação do córtex frontal inferior esquerdo, dos lobos frontal médio e superior direitos, e do lobo parietal inferior direito. Dada a inconsistência de resultados entre estudos, mantém-se em aberto o debate sobre as bases neuronais da categorização de objetos com diferentes graus de tipicidade.

O presente estudo visa investigar a base neural da categorização dos objetos e as regiões cerebrais envolvidas no processamento da tipicidade dos objetos. Espera-se que os objetos não pertencentes à categoria, quando comparados com objetos membros da categoria, evoquem maior ativação no lobo frontal inferior esquerdo e em áreas temporais (ex.: LTA), refletindo processos de categorização semântica. Em relação ao efeito de

tipicidade, foi previsto que itens atípicos, relativamente aos típicos, provocassem uma maior ativação no lobo frontal inferior esquerdo, associado a uma maior exigência no controlo semântico. Em contraste, previu-se que os itens típicos originassem uma maior ativação no lobo parietal inferior e temporal posterior, associados ao processamento e decisão com base na semelhança (mas ver Liu et al., 2013 para um resultado diferente).

Vinte e seis participantes (saudáveis, jovens, estudantes da FP-UL e com o português europeu como língua materna) participaram neste estudo de fMRI. Foram apresentados pares de objeto-categoria e foi pedido aos participantes para decidir se cada objeto pertencia ou não à categoria. Foram utilizadas dez categorias semânticas pertencentes aos domínios de seres não vivos (instrumentos musicais, veículos, utensílios de cozinha, armas, vestuário) e de seres vivos (mamíferos, vegetais, aves, frutos, insetos). O emparelhamento entre a categoria e os objetos permitiu criar um plano fatorial 2x2 com 20 ensaios de itens típicos pertencentes à categoria (ex.: fruto-pêra), 20 ensaios de itens atípicos pertencentes à categoria (ex.: mamífero-morcego), 20 de itens típicos não pertencentes à categoria (ex.: vegetal-casaco) e 20 ensaios de itens atípicos não pertencentes à categoria (ex.: veículo-abacate). A cada participante foram mostrados oitenta ensaios, em dois blocos com uma pausa a meio, e os dados de neuroimagem e os dados referentes às respostas dos participantes (precisão e tempo de resposta) foram registados para análise.

Os resultados comportamentais mostraram um efeito de tipicidade significativo tanto para a exatidão como para os tempos de resposta, replicando, assim, a literatura existente (Alves et al., 2021; Hampton, 1997; Li et al., 2021; Liu et al., 2013; Rosch, 1975). Mais concretamente, os objetos típicos foram categorizados mais rapidamente e com mais exatidão do que os objetos atípicos. Ademais, este efeito foi modulado por uma interação, já que a primazia dos objetos típicos só foi encontrada quando estes pertenciam



à categoria apresentada. O maior tempo de resposta associado aos objetos atípicos tem sido associado à dificuldade em atingir o limiar de semelhança com as características típicas da categoria. Já a exatidão prende-se com a insuficiente identificação de características tipicamente atribuídas à categoria em objetos atípicos (Hampton, 1997).

Relativamente aos dados neuronais, a categorização de objetos não pertencentes à categoria recrutou principalmente o precuneus direito. Esta região tem sido identificada como importante na decisão com base na semelhança (Wirebring et al., 2018). Por serem distintos de objetos que pertencem à categoria, os objetos não pertencentes requerem um maior esforço na decisão com base na semelhança. Já os objetos pertencentes à categoria evocaram ativação na circunvolução medial frontal. O córtex pré-frontal medial tem sido associado à integração de informação nova com informação previamente adquirida pelos sujeitos. Assim, por terem conhecimento relativo à categoria, os participantes conseguem conectar esse conhecimento com um objeto que seja congruente com esta.

No que diz respeito ao efeito de tipicidade, a categorização de objetos atípicos, relativamente a objetos típicos, ativou o lobo frontal inferior esquerdo, associado ao controlo semântico (Novick et al., 2005). A categorização de objeto atípicos pode exigir um nível superior de controlo semântico com fim a ignorar semelhanças com membros de outras categorias e suprimir características tipicamente associadas à categoria que podem estar ausentes nestes objetos. Os objetos típicos, por oposição, recrutaram o lobo parietal inferior direito. Esta região tem sido associada à categorização com base na semelhança, fazendo a integração de diferente informação modal (Grossman et al., 2002). Ademais, tarefas associadas a maior dificuldade têm sido associadas à desativação da circunvolução angular (Lambon Ralph et al., 2016). Assim, os objetos típicos, devido ao seu maior nível de semelhança com o protótipo da categoria, apresentam um nível de dificuldade diminuto quando comparado com objetos atípicos.

Por fim, o efeito de interação confirmou que a circunvolução inferior frontal esquerdo foi a região mais ativada durante o processamento de exemplares atípicos, enquanto o lobo inferior parietal foi mais ativado para objetos típicos. É importante notar que estes efeitos só ocorreram quando o objeto pertencia à categoria, o que demonstra que os efeitos de tipicidade dependem dos processos envolvidos durante a categorização e não daqueles envolvidos na exclusão de um item da categoria.

No seu conjunto, estes resultados apoiam dados anteriores sobre o papel central que a tipicidade dos itens desempenha na categorização semântica. Permitem também esclarecer quais as bases neuronais do sistema semântico e como estas são moduladas pelo grau de tipicidade dos itens.

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## 1. Introduction

Semantic memory refers to the general knowledge about the world, including information concerning facts, ideas, social norms, and concepts (Tulving, 1983). It is central for a variety of cognitive tasks, including language, object processing and decision making. Categorisation is a fundamental process for comprehension and the use of conceptual information, as it allows the organization of the gathered knowledge to establish relations between concepts, and the learning of new concepts (e.g., Barsalou, 1985; Grossman et al., 2002).

It is widely accepted that concepts have a graded category membership. This property has been termed typicality, and it reflects the extent to which an item is representative of a category, with some items being more representative or more typical members of their category than others (Rosch & Mervis, 1975; Woollams, 2012). The notion of typicality is built upon similarity, in particular the degree of overlapping features across two exemplars. Within-category-similarity refers to overlapping features of items from the same category, whereas between-category-similarity denotes feature similarity of items from different categories. For example, for the category “mammal”, a typical item (e.g., dog) shares many features with other category members (e.g., has four legs, has fur, breathes), but shares few features with items that do not belong to the category. In contrast, atypical items (e.g., bat) share few features with members of their category and share more features with members outside of their category (e.g., bats have wings and fly, similarly to birds; Dieciuc & Folstein, 2019; Woollams, 2012).

The typicality effect in categorisation and naming tasks has been vastly demonstrated in the scientific literature. In the healthy population, young participants categorise typical objects more quickly and accurately than atypical items (Rosch, 1975).

Critically, typicality explains performance in these tasks over and above other relevant variables such as item familiarity, word frequency and age of acquisition (Barsalou, 1985; Marques, 2007). In a recent study with healthy older adults, Alves et al. (2021) corroborated the pervasiveness of the typicality effect, by showing that older adults are also better in categorising typical than atypical objects. Interestingly, the extent of the typicality effect diminishes along the lifespan as categorisation of atypical items improves. This reduced typicality effect in the elderly has been linked to richer semantic representations associated with learning experiences acquired along the lifespan (Alves et al., 2021).

Relevant evidence has also stemmed from the neuropsychological literature, particularly work in semantic dementia (SD), a neurodegenerative disorder characterized by the atrophy and hypometabolism of bilateral anterior temporal lobes (ATL) resulting in progressive deterioration of semantic memory (Binder et al., 2009; Lambon Ralph et al. 2016; Patterson, 2007). Patients with SD have difficulties in both verbal and nonverbal tasks. In naming tasks, patients have revealed greater accuracy in naming typical items over atypical items (Woollams et al., 2008). In drawing tasks, it has been shown that patients add erroneous features that make the item more “typical” (e.g., four legs on a duck) and omit distinctive features (e.g., the humps of the camel; Bozeat et al., 2003; Patterson et al., 2007). In a categorisation task, patients mistakenly reject atypical items (e.g., emu in the bird category) and wrongly categorise “pseudotypical” objects, such as indicating that a butterfly is a bird (Mayberry et al., 2011). Furthermore, a transcranial magnetic stimulation (TMS) study, in which repetitive stimulation was applied to the ATL in healthy adults, confirmed the greater difficulty in categorising atypical over typical items when the ATL is temporarily “silenced” (Woollams, 2012). Together, these

studies converge on the importance of the ATL in semantic processing, specifically in forming coherent representations of atypical items and integrating distinctive features.

The typicality effect has also been investigated with event-related potentials (ERP). In two studies, Stuss et al. (1988) and Fujihara et al. (1998) looked at the typicality effect on a category verification task. Using both typical and atypical words, both authors found that the typicality effect is noticeable in the N400 component, with typical items eliciting a smaller amplitude than the atypical ones in the 300ms-500ms time window. The authors argued that typical words were more primed by the target category than atypical words and thus a concept is represented by a prototype, i.e., the central tendency of all members of the category (Fujihara et al., 1998). More recently, Hölzje et al. (2019) investigated the electrophysiological correlates of encoding schema-congruent information, by manipulating the semantic congruency between a superordinate category and an exemplar (mammal-lion vs. mammal-fork) and the level of typicality of the congruent items (mammal-lion vs. mammal-bat). They found that, during retrieval, item recognition was better for congruent items than for incongruent ones, with typicality having no significant effect on performance. For subsequently remembered items, the N400 amplitude during encoding was greater for incongruent items, intermediate for low-typical congruent items, and smallest for high-typical congruent items. Moreover, a late frontal positivity associated with subsequently remembered atypical items was found, which was proposed to be related to the processing of expectancy mismatch.

Even though extensive work confirms typicality as a key dimension in the categorisation and organisation of semantic memory, only recently has typicality begun to be used to understand the neural basis of semantic memory, as previous studies with patients and using TMS have focused primarily on a single brain region, i.e., the ATL. In contrast, fMRI studies allow capturing the activation across the entire brain. In one such

study, Santi et al. (2016) showed that categorisation of typical items by healthy young adults involves the right inferior parietal lobe (IPL) and posterior temporal areas, regions that have been associated with similarity processing and prototype evaluation (Grossman et al., 2002). Categorisation of atypical items, on the other hand, elicited activation at the ATL, associated with the integration of distinctive semantic features (Woollams, 2012), and the bilateral inferior frontal gyrus (IFG), linked to semantic control (Novick et al., 2005). Hence, in addition to semantic representation in the ATL, the authors have argued for the critical role of semantic control in processing atypical items. The low within-category-similarity and high between-category-similarity of atypical concepts presumably requires greater control demands for successful categorisation. Notably, it may involve greater selection demands in order to retrieve the appropriate features of the category (e.g., bats produce milk to feed their young) as well as the inhibition of dominant but irrelevant information (e.g., bats fly).

In another fMRI study with Chinese and English speakers, Liu et al. (2013) investigated the neural underpinnings of processing items that belong vs. do not belong to the category, as well as typical vs. atypical items. They found that, across both Chinese and English speakers, out-of-category items engaged greater activity in several regions of the frontal cortex (including, bilateral superior frontal gyrus, and left middle and IFG), bilateral IPL, and left inferior and middle temporal lobes. The reverse contrast (i.e., items that belong vs. do not belong to the category) did not elicit any significant activation. Moreover, for English speakers, atypical items revealed greater activation in the left IFG, right middle and superior frontal gyri, as well as right IPL. Of note, while engagement of IFG for atypical concepts is in line with the finding of Santi et al. (2016), increased IPL activity is in contrast with that study. Chinese speakers showed no differences between



typical and atypical items, which the authors have interpreted as related to the prevalence and availability of linguistically transparent cues to category membership.

Finally, Iordan et al. (2016) used multivoxel pattern analysis to investigate typicality effects in visual and occipitotemporal (object processing) regions. They found that typical items evoked a neural pattern more similar to the average pattern of the category compared to atypical items, in the lateral occipital complex. Moreover, the authors found a difference in activation favouring atypical items in the caudal inferior parietal lobule. This difference was explained based on additional requirements in processing and correctly categorising atypical items (Iordan et al., 2016).

In sum, the studies that have used typicality to shed light on the neural underpinnings of semantic categorization have been limited to the ATL or have provided conflicting findings (e.g., regarding the role of the right IPL).

The present study aims to investigate the neural basis of object categorisation and the brain regions involved in processing object typicality. To address these issues, an fMRI study was conducted with healthy young adults where participants were presented with a category label (e.g., “mammal”) followed by an exemplar (e.g., “dog”) and had to indicate whether the exemplar belong or not to the category. Category membership (belong vs. do not belong to the category) and typicality (typical vs. atypical) were orthogonally manipulated. A similar experimental design to Santi et al. (2016) was followed. Nonetheless, the present study poses scientific originality by presenting three significant differences from the study of Santi et al. (2016). The first is based on the way typicality is manipulated. Both Santi et al. (2016) and Iordan et al. (2016) used typicality as a continuous measure while in the present study typicality was manipulated in a dichotomous categorical manner (i.e., typical, or atypical). This modification allows one to contrast the neural bases of one and the other type of object. The second difference

concerns the number of semantic categories used, going from four in Santi et al. (2016) to ten in the present study. This addition allows to confirm if the results obtained by Santi et al. (2016) extend to other, more diverse, categories. The third difference relates to the analysis of the typicality effect when the items do not belong to the category. While Santi et al. (2016) and Jordan et al. (2016) restricted the analysis to items that belong to the category, Liu et al. (2013) contrasted the processing of items that belong vs. do not belong to the category. Yet, none of these studies examined how the typicality effect interacts with the item category membership. This is an important question yet to be addressed with fMRI, as most behavioural work has shown an interaction effect: participants are faster and more accurate to categorise typical than atypical objects when these belong to the presented category; yet no typicality effect is observed when the items do not belong to the category. These methodological modifications will make it possible not only to replicate the effects found, but also to extend them to new conditions.

Following Liu et al. (2013), it is expected that items that do not belong to the category elicit greater activation, when compared to their in-category counterparts, in frontal areas including bilateral superior frontal gyrus, left middle and IFG, temporal areas such as left inferior and middle temporal lobes, and bilateral IPL, which may reflect increased demands at the level of categorization processing and/or decision making. Concerning the typicality effect, it is predicted that atypical items (relative to typical) prompt larger activation in bilateral IFG, associated with greater semantic control (notably, inhibition and selection processes) and ATL areas, linked to semantic representation of coherent concepts. In contrast, typical items (compared to atypical) should elicit greater activation in the right IPL and posterior temporal areas, which prior work has associated with similarity processing and prototype evaluation (Grossman et al., 2002; Santi et al., 2016). It should be noted, however, that the activation of the right IPL

is still disputable, as Liu et al. (2013) found an increased activation in the area for atypical, rather than typical items. Importantly, it is anticipated an interaction effect between typicality and category membership, such that the differences between atypical and typical items should only be present when the item belongs to the presented category.

## **2. Method**

### **2.1 Participants**

Twenty-six young adults participated in this study. Participants' age range was 18–29 years old ( $M = 21.46$  years), 20 were females, all were healthy, native speakers of European Portuguese, and right-handed. Participants gave their informed written consent and were awarded a course credit as compensation. This study was approved by the ethics committee of the Faculdade de Psicologia at Universidade de Lisboa.

### **2.2 Material**

Stimuli consisted of 80 exemplars from 10 semantic categories (i.e., 8 exemplars per category), which were drawn from a database of 281 pairs developed by Santi, Raposo, and Marques (2015). Half of the categories belongs to the natural kind domain (mammals, vegetables, birds, fruits, and insects) and the other half to the artifact domain (musical instruments, vehicles, kitchen tools, weapons, and clothes). Category membership and item typicality were orthogonally manipulated. As such, half of the items were paired with their own category, whereas the other half were paired with a different category. Within the items paired with their own category, half were typical members (e.g., weapon-sword) while the other half were atypical (e.g., mammal-bat). Items that were paired with a different category (i.e., non-members of the category) were also typical (e.g., vegetable-coat) or atypical members of their own category (e.g., bird-skis).

Exemplars in the four experimental conditions were matched for familiarity and number of letters ( $p > 0.05$  in all cases; see Table 1). Exemplars in the typical condition were rated as significantly more typical of their category than items in the atypical condition ( $p < 0.001$ ; see Table 1).

**Table 1**

*Mean (and Standard Deviation) of the Typicality Ratings, Familiarity Ratings, and Number of Letters of the Exemplars Used in the Experimental Conditions.*

|                     | Typicality  | Familiarity | No. of Letters |
|---------------------|-------------|-------------|----------------|
| Member Typical      | 6.68 (0.20) | 4.20 (1.03) | 6.65 (2.28)    |
| Member Atypical     | 4.08 (0.93) | 3.93 (0.96) | 6.45 (1.96)    |
| Non-member Typical  | 6.70 (0.22) | 4.16 (1.41) | 6.10 (2.07)    |
| Non-member Atypical | 4.10 (0.96) | 4.46 (1.15) | 7.00 (2.90)    |

### 2.3 Procedure

While in the scanner, participants performed a category verification task. They were shown a category name followed by an exemplar and had to decide if the exemplar belonged or not to the category. The pairing between category membership and typicality resulted in a 2x2 full factorial design with 20 trials per condition.

Every trial started with a fixation cross for 500ms, followed by a visual presentation of the category name, for 750ms, an inter-stimuli interval of 200ms, and, immediately after, an item's name appeared for 2000ms. During this last time frame, participants had to decide if the item belonged to the category by pressing one of two keys mapped for yes or no answers. Participants were instructed to answer as quickly and accurately as possible. Between trials, a random inter-stimuli interval of 1500ms,

2000ms, 2500ms or 3000ms was shown to improve statistical efficiency (Dale, 1999). Each participant saw a total of 80 trials, divided in 2 blocks with a break in between. Presentation and timings were controlled using E-Prime software (Psychology Software Tools, Sharpsburg, USA).

After the category verification task, participants were invited to perform a memory recognition task, in which exemplars shown in the category verification task were presented among novel items, and participants indicated if each exemplar was old or new. The memory recognition task was not analysed under this dissertation and thus no further details will be provided. The work presented here focuses on the category verification task.

Prior to the start of the fMRI session, participants completed an fMRI screening form, were given the instructions for the task, signed the consent form, and carried out a short training block to get used to the task.

## **2.4 fMRI parameters**

The study was carried out at Sociedade Portuguesa de Ressonância Magnética at Hospital da Cruz Vermelha in Lisbon. Participants were scanned using a 3 T Philips MR system with a standard head coil. For the fMRI data acquisition, gradient echo planar imaging (GE EPI) was used with the following parameters: repetition time (TR) = 2000ms, echo time (TE) = 23ms, 34 bottom-up interleaved slices parallel to the AC-PC line, 3mm slice thickness, 0.5mm interslice gap, 2mm x 2mm in-plane resolution, matrix size= 116x115, field of view (FOV) = 23cm x 23cm. Whole brain coverage was achieved in the acquisition. The first 3 volumes were discarded to allow for T1 equilibrium. For anatomical visualisation, T1-weighted anatomical images were collected with 1mm isotropic voxels.

## **2.5 Statistical analyses**

### **2.5.1 Behavioural data**

Accuracy and response times were measured for all trials. Repeated-measures ANOVAs were conducted, using SPSS Statistics software (version 26, IBM Corp., New York, USA), with typicality and category membership as the repeated-measures factors.

### **2.5.2 fMRI data**

#### **2.5.2.1 fMRI data pre-processing.**

The functional data was pre-processed and analysed using the Statistical Parametric Mapping software (SPM12, Wellcome Centre for Human Neuroimaging, London, UK). All images were corrected for realignment, which performs spatial correction of subject motion during the scan, and slice timing, that corrects differences in slice acquisition times. The subsequent steps included: co-registration, which spatially matches the T1 anatomical and functional images; segmentation, that segments the anatomical image into grey matter, white matter, cerebrospinal fluid, bone, soft tissue and air/background; normalization, which matches the subject's images to a canonical echo-planar imaging template; and smoothing, in which an 8mm FWHM Gaussian filter kernel is applied to suppress noise and effects due to residual differences in the images (Penny et al., 2006).

#### **2.5.2.1 fMRI data statistical analyses.**

The data was modelled using the 2x2 full factorial design which yielded four conditions. Following the general linear model, 2 typicality (typical, atypical) and 2 category membership (member, non-member) parameters were included in the model

along with six nuisance regressors for motion parameters. In the first-level analysis, the data from each participant was modelled using the canonical hemodynamic response function and estimation was carried out, leading to estimated parameters for each covariate. Afterwards, contrast files for each condition relative to rest state were generated for use in the second-level analysis. This consisted in a full factorial analysis, which allows to test the main effect of category membership, the main effect of typicality, and the interaction between these factors at the group-level. Statistical maps were thresholded at voxel-wise  $p = .001$  uncorrected, and then clusters that survived  $p < .05$  FWE (family wise error correction) were considered significant.

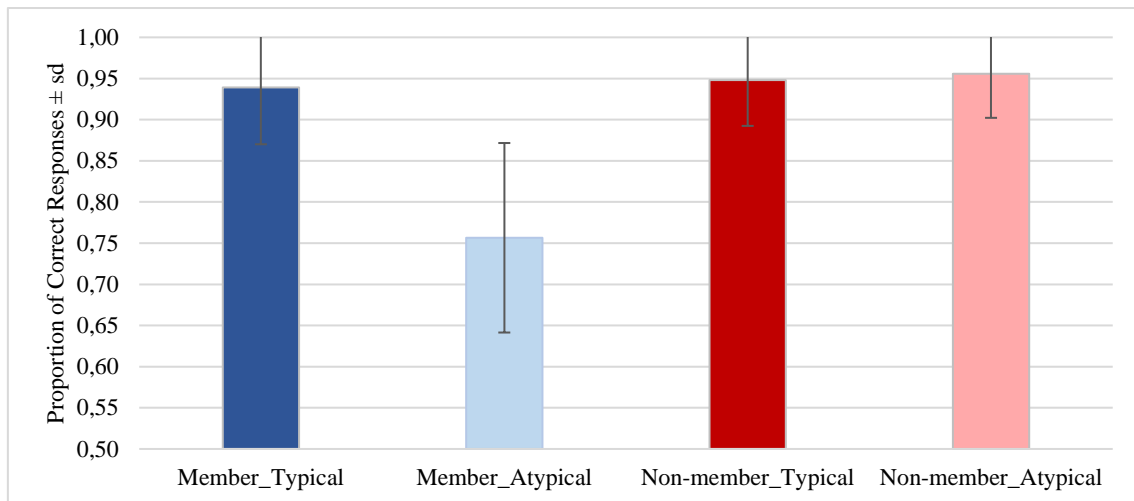
### 3. Results

#### 3.1 Behavioural data

Regarding accuracy (see Figure 1), there was a main effect of category membership as participants were more accurate in responding to items that were not members of the category than to items that were members,  $F(1, 25) = 31.79, p < .001$ . There was also a main effect of typicality, with more accurate responses to typical than atypical items,  $F(1, 25) = 43.761, p < .001$ . Also, an interaction effect was observed with typical items being better categorised than atypical ones when the item belonged to the category, while in the non-member condition no typicality differences were found  $F(1, 25) = 64.43, p < .001$ ).

#### Figure 1

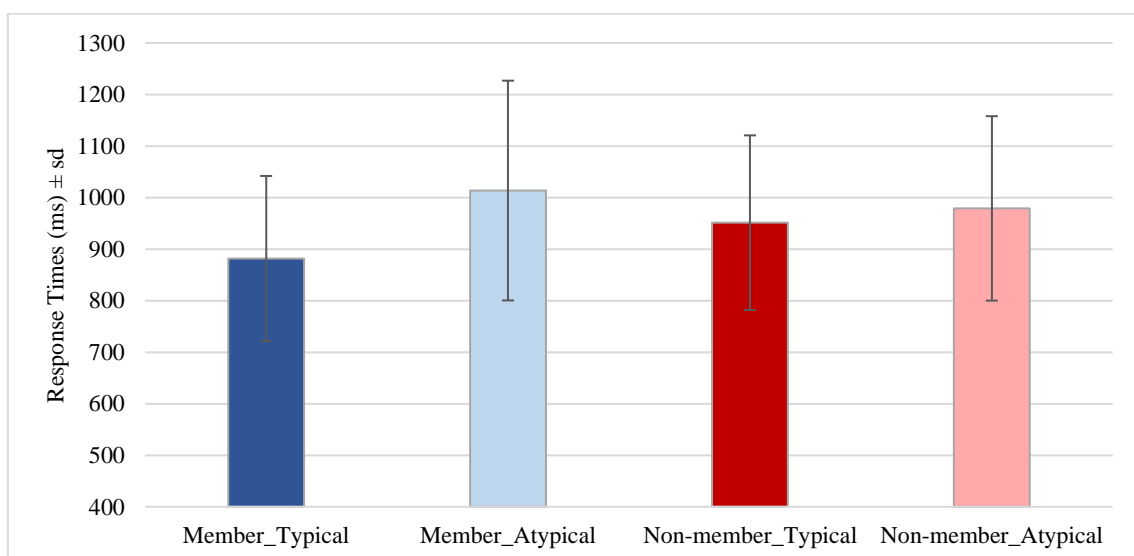
*Mean Proportion of Correct Responses in Each Condition. Error Bars Represent the Standard Deviation.*



In respect to response times (see Figure 2), typical items were categorised faster than atypical items,  $F(1, 25) = 52.933, p < .001$ . This effect of typicality was modulated by a significant interaction that showed that typical items were categorised faster only when the exemplar was a member of the presented category  $F(1, 25) = 22.701, p < .001$ .

## Figure 2

*Mean Response Time for Correct Responses for Each Condition (in ms). Error Bars Represent the Standard Deviation.*





## 3.2 fMRI data

### 3.2.1 Main effect of category membership

Increased activation for items that belonged to the category, relative to items that did not match the category, was observed in three main clusters (Table 2, top panel). One cluster was in the medial frontal gyrus (see Figure 3A) extending to the bilateral supplementary motor cortex, and bilateral anterior cingulate gyrus. Another cluster of activation was also found in the left inferior frontal gyrus (see Figure 3B), including the pars triangularis and pars opercularis. Finally, another cluster was centred in the right caudate, extending to anterior cingulate gyrus and other parts of the basal ganglia area, such as the putamen, the nucleus accumbens and the pallidum.

The categorisation of items that were not members of the presented category, in relation to items that belonged to the category, recruited the right precuneus and cuneus in the occipital lobe, as well as the left caudate nucleus (Table 2, bottom panel).

**Table 2**

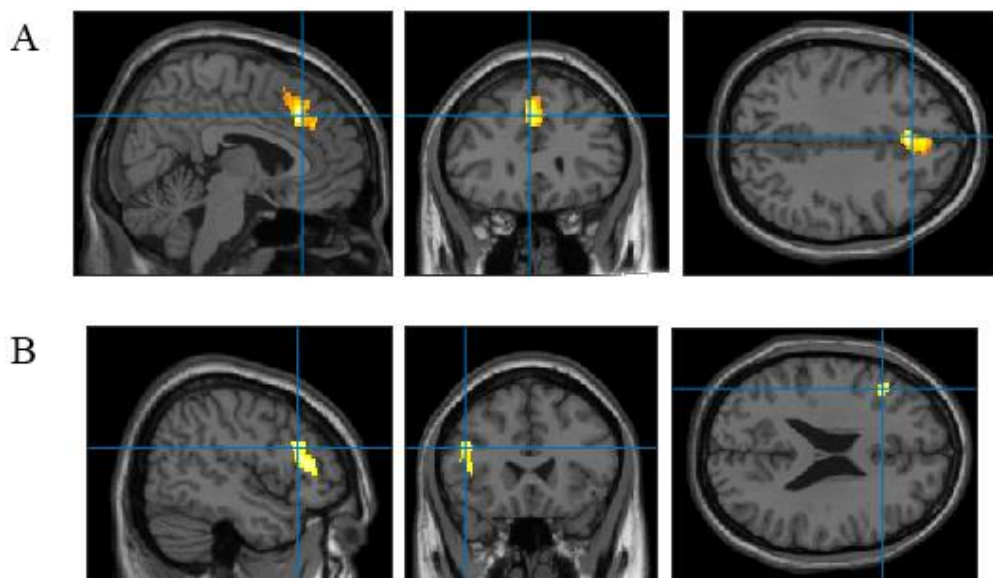
*Category Membership Effect. Regions Demonstrating Increased Activation for Member vs. Non-Member Condition and Vice-versa.*

| <b>Region</b>                        | <b><i>p</i> (FWE-corr.)</b> | <b>No. Voxels</b> | <b>Z</b> | <b>MNI coordinates<br/>(mm)</b> |
|--------------------------------------|-----------------------------|-------------------|----------|---------------------------------|
| <b><i>Member &gt; Non-member</i></b> |                             |                   |          |                                 |
| Left medial frontal gyrus            | <.001                       | 392               | 4.66     | -6, 30, 38                      |
| Right caudate                        | <.001                       | 282               | 4.58     | 10, 16, -7                      |
| Left inferior frontal gyrus          | .001                        | 145               | 4.07     | -48, 24, 23                     |
| <b><i>Non-member &gt; Member</i></b> |                             |                   |          |                                 |

|                 |       |     |      |              |
|-----------------|-------|-----|------|--------------|
| Right precuneus | <.001 | 700 | 4.41 | 18, -64, 26  |
| Left Caudate    | .038  | 73  | 4.04 | -24, -24, 26 |

### Figure 3

*Regions Demonstrating Greater Activation for Member vs. Non-member Condition. A. Activity in the Left Medial Frontal Gyrus (Peak Coordinates [-6, 30, 38]). B. Activity in the Left Inferior Frontal Gyrus (Peak Coordinates [-48, 24, 23]).*



#### 3.2.3 Main effect of item typicality

Categorising typical items, in relation to atypical ones, elicited activation in several clusters as illustrated in Table 3 (top panel). In particular, activation was observed in the right middle and right superior temporal gyrus, extending posteriorly to the angular gyrus (AG; Figure 4A); right middle and superior frontal gyrus; medial frontal gyrus; and bilateral precuneus extending to the posterior cingulate gyrus.

On the other hand, categorising atypical objects, compared to typical ones, recruited a distinct set of regions (bottom panel of Table 3). Notably, the left inferior frontal gyrus (pars opercularis; see Figure 4B), and the left occipital cortex, including the left lingual gyrus and calcarine cortex.

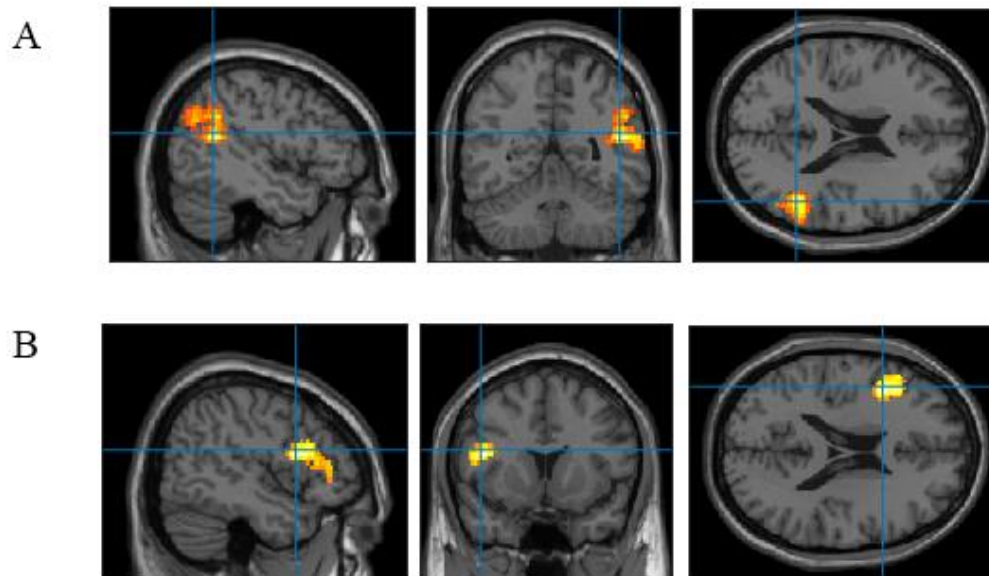
**Table 3**

*Item Typicality Effect. Regions Demonstrating Increased Activation for Typical vs. Atypical Items and Vice-versa.*

| <b>Region</b>                       | <b><i>p</i> (FWE-corr)</b> | <b>No Voxels</b> | <b>Z</b> | <b>MNI coordinates<br/>(mm)</b> |
|-------------------------------------|----------------------------|------------------|----------|---------------------------------|
| <b><i>Typical &gt; Atypical</i></b> |                            |                  |          |                                 |
| Right middle temporal gyrus         | <.001                      | 852              | 5.52     | 46, -52, 20                     |
| Right precuneus                     | <.001                      | 1504             | 5.41     | 2, -44, 44                      |
| Right middle frontal gyrus          | .011                       | 96               | 4.79     | 30, 40, 44                      |
| Right medial frontal gyrus          | .002                       | 131              | 4.21     | 10, 48, -4                      |
| <b><i>Atypical &gt; Typical</i></b> |                            |                  |          |                                 |
| Left inferior frontal gyrus         | <.001                      | 484              | 4.64     | -48, 12, 20                     |
| Left calcarine cortex               | .007                       | 105              | 4.08     | -14, -86, 8                     |

**Figure 4**

*Regions Demonstrating a Main Effect of Typicality. A. Increased Activation for Typical items in the Right Middle Temporal Gyrus (Peak Coordinates [46, -52,20]), extending to the Angular Gyrus. B. Increased Activation for Atypical Items in the Left Inferior Frontal Gyrus (Peak Coordinates [-48, 12,20]).*



### **3.2.5 Interaction between category membership and item typicality**

A significant interaction effect was observed in two regions (Table 4). First, categorisation of typical items (compared to atypical) was associated with stronger activation in the left precuneus (Figure 5A), extending to the left cuneus, when the item belonged to the presented category, while in the non-member condition, no typicality differences were found. Second, an interaction was also found in the inferior frontal gyrus (pars orbitalis), extending to the left anterior insula (Figure 5C), as engagement of this region was greater when categorising atypical items (relative to typical ones) in the member condition only.

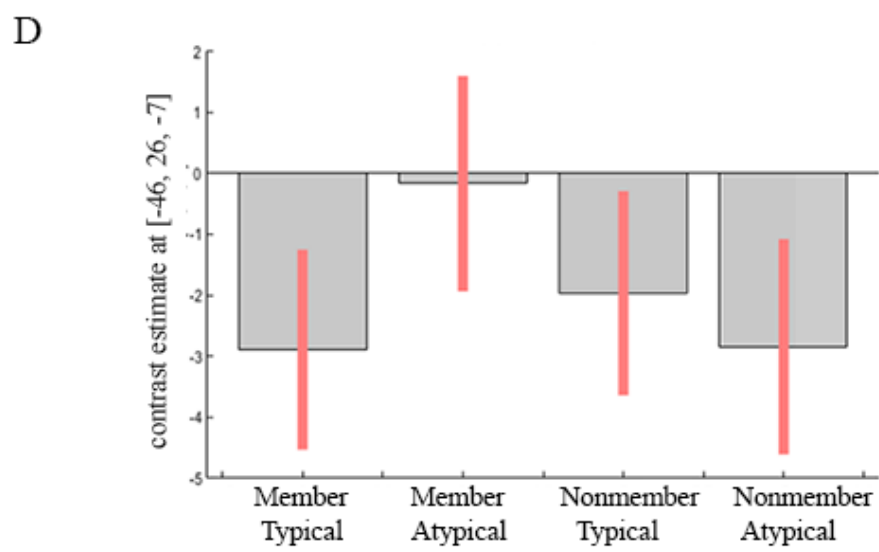
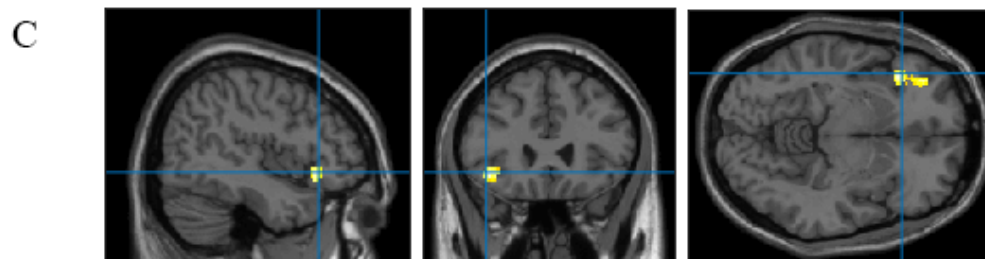
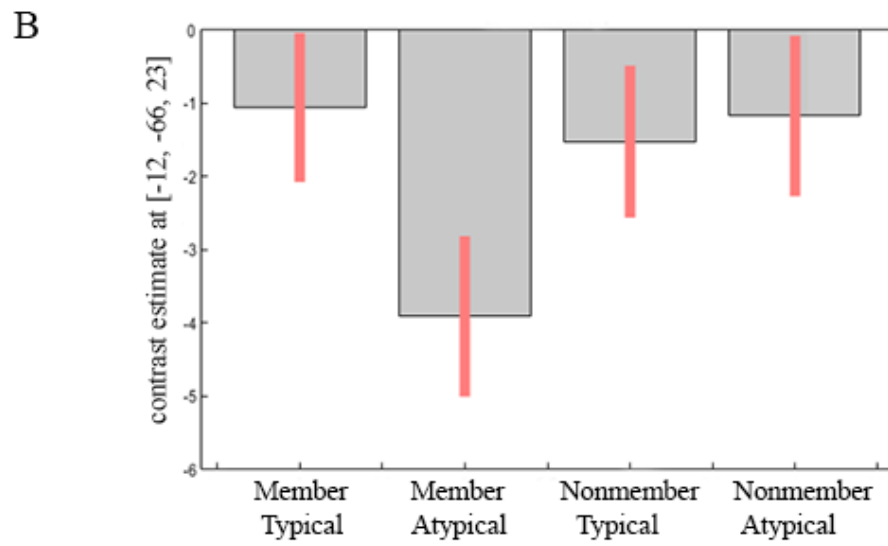
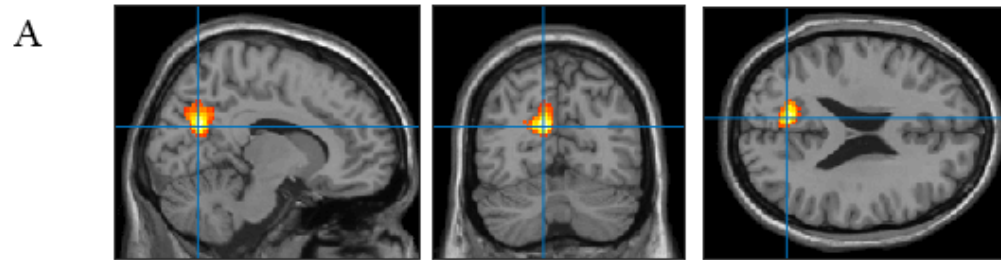
**Table 4**

*Interaction Effect. Regions Demonstrating Increased Activation for Typical vs. Atypical Items and Vice-versa when the Item Belonged to the Category.*

| <b>Region</b>  | <b><i>p</i> (FWE-corr)</b> | <b>No. Voxels</b> | <b>Z</b> | <b>MNI coordinates<br/>(mm)</b> |
|--|----------------------------|-------------------|----------|---------------------------------|
| <b><i>Typical &gt; Atypical Member condition</i></b> |                            |                   |          |                                 |
| Left precuneus                                       | <.001                      | 394               | 5.67     | -12, -66, 23                    |
| <b><i>Atypical &gt; Typical Member condition</i></b> |                            |                   |          |                                 |
| Left inferior frontal gyrus                          | .002                       | 132               | 4.05     | -46, 26, -7                     |

## **Figure 5**

*Regions Demonstrating an Interaction Effect. A. Increased Activation in the Left Precuneus for Typical vs. Atypical Items in the Member Condition. B. Contrast Estimates of the Interaction Effect and 90% Confidence Intervals at the Left Precuneus (Peak Coordinates [-12, -66, 23]). C. Increased Activation in the Left Inferior Frontal Gyrus for Atypical vs. Typical Items in the Member Condition. D. Contrast Estimates of the Interaction Effect and 90% Confidence Intervals at the Left Inferior Frontal Gyrus (Peak Coordinates [-46, 26, -7]).*



#### 4. Discussion

The present fMRI study investigated the neural bases of object categorisation and processing object typicality, by using a category verification task where category membership and item typicality were orthogonally manipulated.

As expected, the behavioural data showed a significant typicality effect for both accuracy and response times: typical items were categorised more quickly and more accurately than atypical items. This effect was modulated by an interaction, as the advantage of typical items was only found when the item belonged to the presented category. These findings replicate extensive evidence in the behavioural literature (Alves et al., 2021; Hampton, 1997; Li et al., 2021; Liu et al., 2013; Rosch, 1975). Categorisation decisions require the comparison of the item's features with the prototypical features of the category. It has been proposed that it takes longer to reach the threshold of similarity to successfully determine that an atypical concept is a member of the category, and hence longer RT are observed (Hampton, 1997). Regarding accuracy, it has been argued that a failure in identifying sufficient shared features between an atypical exemplar and its category underlies the increased number of errors in categorizing atypical objects (Hampton, 1997). The results highlight the relevance of feature similarity in object categorization and, more generally, in semantic processing.

Regarding the imaging data, the current findings differed from those of Liu et al. (2013) who demonstrated that non-members of the category elicited greater activation in frontal, temporal, and inferior parietal areas. In the present study, non-members recruited more restricted regions in right precuneus and cuneus and left caudate nucleus. Activity in the precuneus has been linked with tasks that involve visuo-spatial imagery and episodic memory retrieval (Cavanna & Trimble, 2006), as well as object categorization (Gerlach et al., 2015) and similarity-based judgements (Wirebring et al., 2018). When

participants are presented with a category and an exemplar, they might engage in mental imagery of the objects, which presumably includes the processing of visual features, in order to decide if it belongs to the category. As mentioned earlier, various models base categorization on similarity, assuming that objects belong to the same category because of their similarity (Barsalou, 1985; Hampton, 1997; Rosch & Mervis, 1975). Interestingly, the precuneus has been seen as a key node for similarity-based judgments (Wirebring et al., 2018). Non-members of the category may involve greater demands in similarity-based judgments than members as they are structurally distinct from the category, and hence recruit greater activation in the precuneus.

Categorisation of members that belonged to the category elicited activation of a neural circuit similar to the frontostriatal circuit, as activation in the frontal cortex, supplementary motor cortex, basal ganglia, and anterior cingulate was found. Basal ganglia activation is seen in a variety of categorisation tasks (Seger & Miller, 2010) and the neuropsychological literature has shown that patients with frontal and basal ganglia deterioration (e.g., Parkinson's disease patients) demonstrate deficits in rule-based category learning (Ashby & Maddox, 2005). These areas are not only important for rule-based category learning, but also for the establishment of the category. Initially, categorisation rules seem to rely on the basal ganglia for them to be learnt, however, as a category becomes more consolidated, there is a shift from this area to more frontal areas, despite subjects showing an increase in basal ganglia activity with practice (Helie et al., 2010).

Of note, members of the category showed greater activation in the medial prefrontal cortex (mPFC), a region that has been consistently reported in the schema-based memory literature. Schemas are superordinate knowledge structures responsible for the organisation of lower-level representations from long term memory and, when



activated, they are thought to facilitate encoding, consolidation and retrieval of new information (Gilboa & Marlatte, 2017). The categories used in the present study were quite familiar to the participants and are presumably part of participants' schema (e.g., the schema of a mammal). In an earlier study, van Kesteren et al. (2013) have shown that, during encoding of information, in which participants rated the relationship between objects and scenes, activation of the mPFC positively correlated with the level of congruency. The authors proposed that the mPFC guides integration of new information into a pre-existing schema, which in turn correlates with subsequent memory performance. In the current study, items that belonged to the category recruited the mPFC, which is in agreement with the proposal that this region is important in schema-congruent processing. After seeing a category, participants saw an item. Since this item is a member of the category, it fitted the participants' pre-existing schema, hence the activation of the mPFC. As noted earlier, even though this dissertation focuses on the categorization task, the current study involved a subsequent memory task. This strengthens the view that mPFC plays an important function in the processing of schema congruent information, particularly in the encoding of such information for later retrieval.

Turning to the typicality effects, categorisation of atypical items recruited mainly the left IFG, in line with the findings of Santi et al. (2016) and Liu et al. (2013). The left IFG is thought to be involved in semantic control (Binder et al., 2009; Novick et al., 2005). Including an atypical item in its category might demand additional efforts in semantic control due to the between-category-similarity features. Moreover, seeing a category label first may lead to the creation of an expectation about the type of object that will appear next, which is then in conflict with the presented item. This may require suppressing the predicted typical features of the category in order to successfully categorise atypical exemplars. It should be noted that, in contrast to the established

hypothesis, activation in the ATL for atypical items was not observed. The ATL region has been associated with the representation of concepts, particularly the integration of atypical and distinctive features (Patterson et al., 2007; Santi et al., 2016; Woollams, 2012). The lack of ATL activation may be due to signal distortion and dropout in this region, as revealed by prior work (e.g., Devlin et al., 2000; Visser et al., 2010). Thus, the absence of ATL activation does not mean that this region is not involved in conceptual representation and feature integration.

Concerning the categorisation of typical items, the current results are consistent with the findings of Santi et al. (2016) of increased activation in posterior temporal areas and in right IPL, extending to the AG. Grossman et al. (2002) found significant activation of the IPL in similarity-based categorising tasks, which the authors proposed to be associated with the integration of different modality specific information, coherent with prototypical features. Further, the AG supports the integration and retrieval of complex information by taking part in tasks that require the combination of concepts like sentence comprehension and problem solving (Binder et al., 2009). A more recent review revealed that, in semantic tasks, AG activation correlates inversely with task difficulty (Lambon Ralph et al., 2016). In tasks where subjects were confronted with words versus non-words or concrete versus abstract concepts, increased AG activation was observed for words and concrete concepts over their counterparts, as higher difficulty tasks reveal a deactivation of the area. Task difficulty could explain the disparity in results between Liu et al. (2013) and the present study and Santi et al. (2016). The former used morphological transparent words (i.e., words that contain cues to their category such as basketball and football for the ball category) that facilitated the category verification and diminished the need for semantic control that an atypical item tends to demand. Moreover, a recent study by Li et al. (2021) found greater activation in the right supramarginal gyrus for typical items when

compared to atypical ones, providing further evidence for the role of this area, and/or neighbouring regions, in processing typical items.

Finally, the interaction confirmed that the left IFG was more activated during the processing of atypical exemplars whereas the IPL was more engaged for typical objects. Importantly, these effects only occurred when the item belonged to the category, which demonstrates that typicality effects are dependent on processes engaged during categorisation and not those involved in excluding an item from the category.

The current study presents some limitations. As previously mentioned, activation in the ATL, a core region in the processing of atypical items (e.g., Patterson, 2007; Woollams, 2012) was not observed. This can be explained by technical limitations. In the present study, gradient echo EPI was used for the fMRI data acquisition. This type of imaging sequence is known to be prone to signal loss in regions such as the anterior and inferior temporal lobes and inferior polar region, due to large magnetic susceptibility variation (even though some have been able to find robust activation in this region with this imaging sequence; see Reilly et al., 2018; Visser et al., 2010). Using both spin echo EPI and distortion correction would have minimized this problem. However, spin echo EPI has a lower sensitivity to hemodynamic activation and temporal resolution than gradient echo EPI (Visser et al., 2010). Also, a prior study has suggested that spin echo may reduce activation in other critical regions, such as the IFG (Halai et al., 2014). Future work using dual gradient-echo and spin-echo EPI should be promising in investigating the current issues, as both Halai et al. (2014) and Jackson et al. (2016) found activation in IFG and ATL using dual echo EPI.

Another limitation relates to the notion of typicality in the non-membership condition. If one defines typicality as the extent to which an item is representative of a category, then it can be argued that, if an item is not a member of a category, it cannot be

typical or atypical. This is in line with the study of Höljtje et al. (2019), as the authors only considered three conditions (high typicality, low typicality and incongruent). Nevertheless, as exemplars in the typical condition were rated as significantly more typical of their category than items in the atypical condition, it was reasoned that such differences in typicality may affect not only the attribution of an item to the category, but also the rejection of an item as a member of another category.

Lastly, the present work focused on the categorisation of items. Yet, the study also involved a recognition memory task. Future analyses should explore schema-based memory and its role in item recognition. Van Kesteren et al. (2013) and Höljtje et al. (2019) found that congruent items (typical and atypical) are better remembered than incongruent ones. However, the neural underpinnings of typicality in schema-based memory remain unclear. In this direction, Höljtje et al. (2019) found a late frontal positivity associated with subsequently remembered atypical items. The authors proposed that this late activity is related to the processing of expectancy mismatch, which may be linked to the left IFG activation found in our study during the categorisation of atypical items. Nevertheless, further studies are required to further understand how the ERP findings of Höljtje et al. (2019) translate into fMRI. Similarly, van Kesteren et al. (2013) found greater mPFC engagement during encoding of semantically congruent information which in turn resulted in superior memory for semantically congruent items. It would be relevant to investigate how this effect is modulated by the item's typicality.

## **5. Conclusion**

Exploring the brain areas involved in the processing of concept typicality allows for a better understanding of the neural bases of semantic memory. The present data supports the involvement of the IPL in the processing of typical items, associated with

the integration of prototypical features and task difficulty. Atypical items, on the other hand, recruited the IFG, which is thought to be related with greater semantic control demands. These effects were restricted to the condition where the item was a member of the category of the presented category, thus showing that typicality effect affects the process of categorisation. This study contributes to a growing body of work demonstrating the critical role of typicality in semantic categorization and conceptual processing.

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