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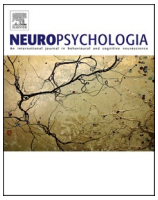

Semantic cognition in healthy ageing: Neural signatures of representation and control mechanisms in naming typical and atypical objects

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ABSTRACT

Effective use of conceptual knowledge engages semantic representation and control processes to access information in a goal-driven manner. Neuropsychological findings of patients presenting either degraded knowledge (e.g., semantic dementia) or disrupted control (e.g., semantic aphasia) converge with neuroimaging evidence from young adults, and delineate the neural segregation of representation and control mechanisms. However, there is still scarce research on the neurofunctional underpinnings of such mechanisms in healthy ageing. To address this, we conducted an fMRI study, wherein young and older adults performed a covert naming task of typical and atypical objects. Three main age-related differences were found. As shown by age group and typicality interactions, older adults exhibited overactivation during naming of atypical (e.g., avocado) relative to typical concepts in brain regions associated to semantic representation, including anterior and medial portions of left temporal lobe (respectively, ATL and MTG). This provides evidence for the reorganization of neural activity in these brain regions contingent to the enrichment of semantic repositories in older ages. The medial orbitofrontal gyrus was also overactivated, indicating that the processing of atypical concepts (relative to typical items) taxes additional control resources in the elderly. Increased activation in the inferior frontal gyrus (IFG) was observed in naming typical items (relative to atypical ones), but only for young adults. This suggests that naming typical items (e.g., strawberry) taxes more on control processes in younger ages, presumably due to the semantic competition set by other items that share multiple features with the target (e.g., raspberry, blackberry, cherry). Together, these results reveal the dynamic nature of semantic control interplaying with conceptual representations as people grow older, by indicating that distinct neural bases uphold semantic performance from young to older ages. These findings may be explained by neural compensation mechanisms coming into play to support neurocognitive changes in healthy ageing.

1. Introduction

The effective use of conceptual knowledge allows us to properly interact with objects and communicate with others. Previous research has suggested that our semantic cognition entails at least two mechanisms: the semantic representation of objects and their features, developed across heterogenous experiences throughout the lifespan, and the capacity to exert semantic control over the assembled representations to retrieve and select task-appropriate knowledge (Hoffman, 2018; Jefferies, 2013; Lambon-Ralph, 2014; Lambon-Ralph et al., 2017). Converging neuroimage evidence have shown that, despite interacting dynamically to support behaviour, semantic representation and control mechanisms engage distinct brain regions.

Studies with healthy young adults, using functional Magnetic Resonance Imaging (fMRI) and Transcranial Magnetic Stimulation (TMS), have provided evidence that the anterior temporal lobes (ATL) receive multimodal inputs from different sensory-motor areas distributed across the cortex (Chiou et al., 2018; Chiou and Lambon-Ralph, 2019; Pobric et al., 2010; Visser et al., 2012). This supports the role of the ATL in extracting regularities from items over context-dependent experiences to form coherent semantic representations and promote generalizations that go beyond objects' surface (dis)similarities (Lambon-Ralph, 2014; Lambon-Ralph et al., 2017; Martin et al., 2018; Patterson et al., 2007). Such semantic mechanism harnessed at anterior portions of ventral pathways assumes a suitable position to distil information of the typical location and use of objects (Peelen and Caramazza, 2012) as well as their

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semantic features (Jackson et al., 2015; Lewis et al., 2015; Teige et al., 2019) across various tasks (Lambon-Ralph et al., 2017; Martin et al., 2018; Patterson et al., 2007). This evidence embeds the hub-and-spoke model (see Lambon-Ralph et al., 2017; Patterson et al., 2007), and provides insight into semantic dementia (SD), a neurodegenerative disorder affecting primarily the ATL. Critically, SD patients have been characterized by the degradation of semantic representations, with a consistent loss of specific and atypical concepts features, while more general and typical feature knowledge remains relatively preserved in the early stages of the disease (Lambon-Ralph et al., 2017; Marques and Charnallet, 2013; Mayberry et al., 2011; Patterson, 2007; Rogers et al., 2015; Woollams et al., 2008).

Semantic control, on the other hand, has been associated to the functioning of the inferior frontal gyrus (IFG; Badre and Wagner, 2002, 2007; Kan and Thompson-Schill, 2004; Thompson-Schill et al., 1997) and, more recently, to the posterior middle temporal gyrus (pMTG; Jefferies, 2013; Visser et al., 2012). Both regions have shown increased activation when semantic control demands are high (e.g., deciding whether salt-grain are related as opposed to salt-pepper) and such processing is disrupted after inhibitory stimulation of these regions (Davey et al., 2016; Noonan et al., 2013; Whitney et al., 2011). It has thus been proposed that semantic control in IFG and pMTG may be relevant to identify semantic relationships between distinct concepts (e.g., mouse and elephant are both mammals) by directing retrieval and selection processes towards shared features while discarding divergent ones (Jackson et al., 2015; Jefferies, 2013; Jefferies et al., 2020). These studies are consistent with the control deficits exhibited by patients diagnosed with semantic aphasia (SA) after vascular lesions within the fronto-parieto-temporal language network (Corbett et al., 2011; Jefferies and Lambon-Ralph, 2006; Rogers et al., 2015). Contrasting to SD, the difficulties of SA patients in identifying features linking less related concepts (e.g., pliers-tweezers) seem due to task control demands to solve the semantic competition imposed by non-target items (e.g., lipstick, nail varnish, hairbrush) rather than to the erosion of knowledge content *per se* (Jefferies and Lambon-Ralph, 2006).

Yet, little is known about the functional neuroanatomy underlying such interactive mechanisms in healthy ageing, which has been linked to neurocognitive changes affecting particularly prefrontal functioning (Cabeza et al., 2018; Hasher et al., 2007; Hedden and Gabrieli, 2004; Lustig et al., 2008; West, 1996; Zanto and Gazzaley, 2017). In the present fMRI study, we investigate potential changes in semantic representation and control mechanisms during naming of typical and atypical objects in ageing. In the following sections, we first address the representation of concept typicality and how it interacts with control demands of semantic tasks. We then discuss the implications of neurocognitive ageing in conceptual processing.

1.1. Semantic representation and control in processing typical and atypical concepts

Concept typicality has been key to study semantic representation. It refers to the degree of interrelated features (e.g., shape, colour, size) shared between concepts organized into higher-order categories based on their similarity (Rogers and McClelland, 2004; Rosch, 1975; Rosch and Mervis, 1975). Within the mammal category, for instance, some items (e.g., whales) share few features with the respective coordinate members (e.g., elephants) and share many features with members of other categories (e.g., fish). Hence, they are considered more atypical category exemplars. Such pattern of feature sharedness yields atypical concepts as structures of less interrelated features (Woollams, 2012) and more distant from other category members (Rogers and McClelland, 2004; Rogers et al., 2015). This results in the typicality effect being observed primarily in category-identification tasks, with young and older participants taking longer and often being less accurate in categorizing atypical (i.e., deciding that a whale is a mammal) relative to typical items (i.e., deciding that an elephant is a mammal) (Alves et al., 2021; Hampton, 1997; Hoffman et al., 2013; Kiran and Thompson, 2003; Kiran et al., 2007; McCloskey and Glucksberg, 1979; Räling et al., 2015, 2016, 2017; Sandberg et al., 2012; Santi et al., 2016). Interestingly, in categorization tasks both SD and SA patients present exacerbated typicality effects (Rogers et al., 2015), suggesting that the inclusion of atypical concepts in the appropriate categories relies on intact semantic representations and functional control mechanisms.

Prior work has provided support for the role of the ATL in the semantic representation of atypical concepts, while also clarifying the involvement of semantic control processes. In a TMS study with healthy young adults, Woollams (2012) showed that temporary lesions induced at the ATL elicited difficulties in naming pictures of atypical compared to typical objects. This pattern mimics the behaviour of SD patients who show exacerbated typicality effects in naming tasks, consistent with the loss of the less interrelated features of atypical items (Hodges et al., 1995; Rogers and Patterson, 2007; Rogers et al., 2015; Woollams, 2012; Woollams et al., 2008). In the same line, using whole-brain fMRI, Santi et al. (2016) revealed that semantic categorization of atypical concepts activated the ATL. Importantly, such activation was accompanied by increased engagement of the IFG, suggesting that the successful categorization of atypical items requires semantic control. Typical concepts, on the other hand, activated a large set of temporoparietal regions, notably the inferior parietal gyrus and the pMTG (Santi et al., 2016). Together, these studies indicate that the ATL plays a critical role in the representation of atypical concepts and their less interrelated features across naming and categorization tasks.

In the realm of object processing studies, it has been shown that identifying objects at higher-order domain (e.g., living thing) or at a more specific level (e.g., zebra) recruits different brain regions (Clarke, 2019; Clarke et al., 2011; Clarke and Tyler, 2015; Moss et al., 2005; Taylor et al., 2007; Tyler et al., 2004a,b). While occipitotemporal areas were involved in object naming regardless of the level of specificity required, left anteromedial temporal structures were recruited during specific level naming, which suggests that the anteromedial temporal cortex is critical for the detailed discrimination of objects that share similar features (e.g., distinguishing a zebra from a horse; Clarke, 2019; Clarke et al., 2011; Clarke and Tyler, 2015; Moss et al., 2005; Taylor et al., 2007; Tyler et al., 2004a,b). Magnetoencephalography (MEG) studies have showed that the ATL and posterior visual areas within the ventral stream are involved in the early stages of concept processing (150 ms after stimulus onset), wherein coarse-grained processing is thought to occur to extract category-related information (Clarke, 2019; Clarke and Tyler, 2015). There is also evidence of the involvement of ATL (Mollo et al., 2018) and medial temporal lobe (MTL) structures (Clarke, 2015; Clarke et al., 2018) in processing fine-grained concept representations, thought to take place around 250 ms after stimulus onset to extract object-related information (Clarke, 2019; Clarke and Tyler, 2015). This clarifies the role of ATL across object identification levels, further indicating a specific contribution of MTL in naming objects at the specific-level.

Similarly, the engagement of brain regions associated to semantic control is susceptible to the demands of task specificity. By virtue of their pattern of feature sharedness, atypical concepts place greater control demands (Rogers et al., 2015) in retrieving their few category-related features (e.g., whales breastfeed their offspring) and inhibiting the features shared with other categories (e.g., whales swim), processes that are particularly relevant in category-verification tasks. On the contrary, naming tasks require instead the differentiation of a given object among similar ones by providing its specific name (Clarke, 2019; Clarke et al., 2011; Clarke and Tyler, 2015; Moss et al., 2005; Taylor et al., 2007; Tyler et al., 2004a,b). In such tasks, the features of typical items are presumably more prone to activate similar objects (e.g., a picture of cat activates similar concepts such as dog, tiger or lion). Conversely, the pattern of less interrelated features of atypical concepts may provide less competition and tax less on control abilities to access the object name (Rogers et al., 2015). According to this view, increased activation in IFG

and/or pMTG should be observed during naming of typical relative to atypical concepts due to greater competition and selection demands, in contrast to what has been reported for categorization tasks (e.g., Santi et al., 2016). This also offers a compelling explanation for the inconsistent behaviour of SA patients reported by Rogers et al. (2015), with impaired performance in categorizing atypical objects but no evidence of typicality effects in naming the same set of objects.

1.2. Cognitive and neural changes in semantic processing along healthy ageing

A well-established observation is that semantic knowledge remains preserved and even increases in healthy adults until later stages of life, despite the earlier decline taking place over other domains. Compared to younger counterparts, older adults present similar abilities in naming objects (Baciu et al., 2016; Belke and Meyer, 2007; Berlingeri et al., 2010, 2013; Ferré et al., 2020; Hoyau et al., 2018), identifying semantic relationships (Maintenant et al., 2011; Peelle et al., 2013; Pennequin et al., 2006), categorizing concepts (Alves et al., 2021; Kiran et al., 2007; Kiran and Thompson, 2003; Räling et al., 2015, 2016, 2017; Sandberg et al., 2012), and processing abstract words (Lacombe et al., 2015). Moreover, several studies have reported that in semantic tasks older adults match younger participants not only in accuracy, but also in response times, even when there is a generalized slowdown in processing speed (Baciu et al., 2016; Berlingeri et al., 2010, 2013; Hoffman, 2018; Hoyau et al., 2018). Furthermore, in knowledge retrieval tasks (e.g., providing word definitions), older adults often exhibit larger and richer semantic repositories relative to younger adults (Hoffman, 2018; Salthouse, 2004, 2019; Verhaeghen, 2003). For instance, older adults outperformed younger counterparts in identifying features (e.g., white) linking less related concepts (e.g., salt-dove), an ability that was positively associated with knowledge breadth in both age groups (Hoffman, 2018). This suggests that the effective retrieval of less related conceptual features is enhanced in healthy adults with detailed semantic repositories, which tend to enlarge as people grow older.

Despite equivalent behavioural performance, fMRI studies have reported age-related differences in semantic processing, revealing both patterns of under- and over-activation in ageing brains, depending on the task at hand. For instance, similar networks have been found during semantic processing across age groups (Baciu et al., 2016; Hoffman and Morcom, 2018). There is also evidence that older adults over-recruit the left ATL under categorization (Ansado et al., 2013) and concreteness decisions (Lacombe et al., 2015). Besides, it has been shown that older adults exhibit more bi-directional connectivity between left IFG and regions in left MTL during naming, while their younger counterparts exhibit preferential connections between left IFG and left lateral temporal lobe regions (Hoyau et al., 2018). These age-related differences may comprise a strategy to maintain efficient semantic performance in older ages in the face of neurofunctional decline and/or a neurofunctional reorganization of semantic representations due to knowledge enlargement (Ansado et al., 2013; Hoyau et al., 2018; Lacombe et al., 2015).

Critically, the age-related changes reported in the structure and function of prefrontal regions support the view of lower cognitive control abilities in older ages. The reduction of cortical volume in this brain region is one of the key signs of the ageing brain (Kennedy and Raz, 2009; Nordahl et al., 2006; Raz et al., 2005), although increasing prefrontal activity is still observed from young to older ages (Cabeza and Dennis, 2013; Grady, 2012; Hedden and Gabrieli, 2004; Park and Reuter-Lorenz, 2009; Reuter-Lorenz and Cappell, 2008). This effect has been attributed to compensatory shifts thought to uphold performance of older adults, counteracting the lifelong neurofunctional decline in structures elsewhere in the brain (Cabeza et al., 2018; Grady, 2012; Hedden and Gabrieli, 2004; Park and Reuter-Lorenz, 2009; Spreng et al., 2010). Greater activity is often presented as an upregulation of cognitive control resources (Cabeza et al., 2018), with older adults overrecruiting the same prefrontal subregions as young adults for similar task conditions (Cabeza et al., 1997; Davis et al., 2008; Grady et al., 1994). Concurrently, older adults may engage other subregions not recruited by younger participants, resulting in the bilateral reorganization of prefrontal activity for older adults in subregions that show a unilateral activation pattern for young adults under the same experimental trials (Berlingeri et al., 2010, 2013; Cabeza, 2002; Cabeza et al., 2002). Alternative accounts propose, however, that widespread activation and the recruitment of additional areas may correspond instead to non-specific (Logan et al., 2002) or inefficient (Zarahn et al., 2007) neural responses of older adults, especially without evidence of behavioural improvements. This may occur due to reduced capacity in processing load (Reuter-Lorenz and Cappell, 2008; Zarahn et al., 2007) or in shifting from default-to task-mode in older ages (Grady, 2012; Park and Reuter-Lorenz, 2009). According to these dedifferentiation accounts, Hoffman and Morcom (2018) have suggested that older adults may recruit other domain-general control regions located in the right hemisphere, such as the right IFG, during inefficient semantic processing. In such case, this would comprise a less efficient strategy to overcome the potential neurofunctional decline from young to older ages in more semantic-specific brain regions, such as the left IFG. Given these multiple accounts, it is unclear how semantic control mechanisms associated with naming objects varying in typicality manifest in the older brain.

1.3. Current study

In this fMRI study, we investigated the neural underpinnings of object naming in young and older adults. By manipulating concept typicality, we inspected how brain regions involved in semantic representation and control interact along age.

Increased ATL activation is expected during naming of atypical relative to typical concepts, in line with the view that the ATL supports the processing and integration of less interrelated semantic features (Rogers et al., 2015; Santi et al., 2016; Woollams, 2012). Since semantic representation tends to be preserved and even incremented in healthy ageing (Alves et al., 2021; Hoffman, 2018), we hypothesise that greater ATL recruitment for atypical than typical objects will be larger for the older group, reflecting the increased ability of older adults to integrate the less interrelated features of atypical items. Additionally, we anticipate that naming typical objects will place greater selection/inhibition demands than naming atypical concepts, thus eliciting more activation in IFG regions, consistently with the view that greater similarity among typical objects enhances competition and taxes cognitive control in naming tasks (Rogers et al., 2015). If the pMTG plays similar control functions as argued earlier (Davey et al., 2016; Jefferies, 2013; Jefferies et al., 2020; Whitney et al., 2011), then we expect typical objects to elicit greater activation in pMTG too. Critically, we predict that the control mechanisms associated with naming typical objects will interact with age. One hypothesis is that, relative to young participants, older adults will show decreased activation (i.e., under-recruitment) of the IFG during naming of typical objects due to lower cognitive control abilities (Park and Reuter-Lorenz, 2009; Reuter-Lorenz and Cappell, 2008). Yet, if spared neural resources are available at older ages to be allocated into demanding situations (Cabeza et al., 1997; Davis et al., 2008; Grady et al., 1994), then older adults may overrecruit the left IFG compared to younger adults. Alternatively, if processing capacity is attenuated, older adults may exhibit instead a bilateral overactivation pattern by recruiting the right portions of IFG (Berlingeri et al., 2010, 2013; Cabeza, 2002; Cabeza et al., 2018).

2. Methods

2.1. Participants

Fourteen young adults (19–28 years old, mean age = 22.5; 9 females) and sixteen older adults (58–76 years old; mean age = 65.2; 12 females)

participated in this study. All were native speakers of Portuguese, right-handed, and had normal or corrected to normal vision. None reported a history of neurological or psychiatric disorders or taking medication that might affect cognitive function. Cognitive decline was screened by applying a cut-off score below 22 points in the Montreal Cognitive Assessment (MoCA) test, according to Portuguese normative data (Freitas et al., 2012). One older participant was excluded following this criterion. Demographic information is presented in Table 1. Young and older adults were recruited from the university and senior university communities, representing a well-educated segment of the population, with no significant difference in years of formal education between groups (t (25,33) = 0.93, $p > .4$). All participants provided written informed consent and were compensated for their time. The protocol was approved by the Ethics Committee of Faculdade de Psicologia, Universidade de Lisboa (FP-ULisboa).

2.2. Materials and procedure

2.2.1. General cognitive assessment

Young and older participants performed a set of neuropsychological tests before the scanning session, following the protocol implemented by Alves et al. (2021). Detailed information was provided about the entire procedure and practice trials were performed before testing. The MoCA test was used for assessing global cognitive capacity. This brief application tool assesses multiple cognitive domains and is advisable to detect mild ageing impairments in well-educated samples (Freitas et al., 2011; Nasreddine et al., 2005). All older adults included in this study scored 22/30 or above, being within the range of non-pathological ageing (cut-off: <22) established for the Portuguese population (Freitas et al., 2012). Semantic memory was examined in both verbal and non-verbal modalities. Verbal semantic ability was assessed using the Vocabulary subtest of the Portuguese version of Wechsler Adult Intelligence Scale (WAIS; Wechsler, 1997), in which participants were asked to verbally define several concepts. Non-verbal semantic abilities were assessed using the picture version of the Camel and Cactus Test (CCT), adapted to the Portuguese language (Fonseca et al., 2016). Participants had to select, among four possible alternatives (one target and 3 distractors), the picture depicting the object sharing a semantic relation with the probe image. Answers were given through button-press. Additional measures were retrieved from Alves et al. (2021) to qualify each CCT trial on three distinct semantic factors (measured in a 7-point scale) as proposed by Jefferies and Lambon-Ralph (2006): 1) the easiness understanding the semantic relationship between probe-target items; 2) the strength of the relationship based on the frequency of probe-target co-occurrence in the same context; and 3) the difficulty in solving the semantic competition exerted by foil items.

Table 1
Mean (standard deviation) of demographic characteristics, neuropsychological test scores and structural brain measures for young and older participants.

	Young		Old
	Mean (SD)		Mean (SD)
Age [years]	22.50 (2.07)	***	65.20 (5.00)
Schooling years	16.29 (1.64)		15.60 (2.30)
MoCA/30	27.14 (1.99)		25.93 (2.49)
Executive/13	11.36 (1.33)		11.80 (1.42)
Visuospatial/7	6.36 (0.75)		6.27 (1.03)
Language/6	5.50 (0.65)		5.60 (0.51)
Attention/18	17.86 (0.36)		17.27 (1.03)
Memory/15	12.79 (2.01)	*	10.20 (4.02)
Orientation/6	6.00 (0.00)		6.00 (0.00)
Vocabulary WAIS/20	15.86 (1.74)		16.13 (2.14)
CCT	.89 (0.07)		.89 (0.08)
Grey matter	824,351 (35,603)	***	725,352 (42,802)
White matter	793,367 (23,871)		784,531 (38,908)

Note. Asterisks indicate statistically significant differences between age groups: *p < .05, ***p < .001.

2.2.2. Object naming task

Fifty-six pictures of objects were evenly selected from four categories used in previous studies (see Alves et al., 2021; Santi et al., 2016), including two natural kind categories (mammals and fruit) and two artefact categories (vehicles and clothing). Typicality values of the concepts that the objects denoted (measured in a 7-point scale) were retrieved from Santi et al. (2016). The median split of values was used to set groups of atypical and typical items (cut-off: 5.60). Half of the pictures corresponded to atypical objects (e.g., olive; $M = 4.02$, $SD = 1.14$), while the other half depicted typical objects (e.g., apple; $M = 6.47$, $SD = 0.38$; t (54) = −10.84, $p < .001$). Typical and atypical objects were matched in a set of variables (all pairwise t-test comparisons, $p > .1$), including familiarity (Santi et al., 2016), log frequency (SUBTLEXPT database from Soares et al., 2015), and number of letters. Moreover, typical and atypical objects were matched in name agreement, and visual complexity of the pictures, as determined by a pre-test in which an independent group of participants ($n = 37$, 31 females, age: $M = 20.22$, $SD = 5.90$) indicated the name of each object and rated how complex each image was using a 7-point scale. Descriptive statistics of all items' properties are presented in Table 2 (see Supplementary Materials for a graphical representation of the distribution of all semantic measures).

While in the scanner, participants performed a covert picture naming task. Each trial began with a fixation cross (500 ms), followed by the presentation of a picture (3500 ms). During picture presentation, participants had to silently name the object at the basic level (e.g., skirt) and then press a button with the left index finger. Successive trials were separated by a variable inter-trial interval (assuming values of 1500, 2000, 2500, or 3000 ms in the proportion of 0.25 each) in order to optimize statistical efficiency. The stimuli were presented in a pseudo-randomized order, such that no more than three objects of the same category were presented in an event-related sequence. Presentation and timing were control using the E-Prime software (http://www.psnet.com/). The task lasted less than 6 min. To check if the name of the objects was easily recognizable, immediately after the scanning session, participants were presented with the same set of images and asked to verbally name each object. Alternative names were considered correct whenever used interchangeably in the Portuguese language. For instance, "raincoat" and "coat" were accepted for *overcoat*. "Shirt" was accepted for *blouse*. It is important to note that older adults exhibited tip-of-tong effects (e.g., "is a, is a … lion") and tended to produce coordinate errors before providing the correct response (e.g., "grapes, no blueberries"), while young adults did not show such behaviour.

2.2.3. MRI acquisition and preprocessing

Whole-brain imaging was conducted on a 3 T Philips MRI system (Philips Medical Systems, Best, NL) using a standard head coil at Sociedade Portuguesa de Ressonância Magnética. High-resolution T1-weighted structural images (3D TFE sequence, TR = 11 ms, TE = 4.6, flip angle = 8°, FOV = 256 × 256 × 160 mm^3, sagittal orientation, voxel size = 1 × 1 × 1 mm^3, total acquisition time = 5.38 min) were acquired for each participant. Immediately after, the fMRI data were acquired using a multi-slice 2D echo-planar imaging (EPI) sequence (TR = 2000 ms, TE = 23, 34 slices parallel to the AC-PC line acquired in a bottom-up interleaved order, with voxels, 3.0 mm thick, interslice gap of 0.5 mm, 2.0 mm × 2.0 mm^2 in-plane resolution, FOV = 23 × 23 cm^2, number of volumes = 159, total acquisition time = 5.32min). Three dummy volumes were discarded to allow for T1 equilibration effects.

Structural image analysis was performed using the FMRIB's Software Library (FSL) software (www.fmrib.ox.ac.uk/fsl). Global brain volume was estimated for each participant from the T1-weighted structural images using of FSL's tool SIENAX (Version 5.0.1). First BET (FSL's Brain Extraction Tool) was used to strip-off non-brain tissue. Skull and brain measures were used to estimate the scaling factor between the subject

Table 2
Mean (standard-deviation) and range of items' characteristics used in the naming task.

	Typicality (1–7)	Familiarity (1–7)	Frequency (Log)	Number of letters	Name Agreement (1–7)	Visual Complexity (1–7)
Typical						
Mean (*SD*)	6.47 (0.38)	4.64 (1.00)	1.87 (0.63)	6.00 (1.83)	0.86 (0.23)	3.56 (1.14)
Range	5.67–7	2.97–6.55	0.70–2.87	4–11	0.14–1.00	1.95–5.49
Atypical						
Mean (*SD*)	4.02 (1.14)	4.25 (1.21)	1.62 (0.55)	6.43 (1.97)	0.85 (0.21)	3.24 (0.88)
Range	1-92–5.58	2.76–6.14	0.30–2.43	4–13	0.14–1.00	1.57–5.05

image and the standard MNI space. FAST (FMRIB's Automated Segmentation Tool) was then used to segment grey matter, white matter, and Cerebrospinal fluid (CSF). Volume estimations were normalized to reduce head-size variability.

Functional image analysis was performed using the Statistical Parametric Mapping software (SPM12, Wellcome Institute of Cognitive Neurology, http://www.fil.ion.ucl.ac.uk/), implemented in Matlab (Mathworks Inc., Sherborn MA, USA). Slice acquisition timing was corrected by resampling all slices in time relative to the middle slice collected, followed by rigid body motion correction. Functional data were spatially normalized to a canonical echo-planar imaging template using a 12-parameter affine and nonlinear transformation. T1-weighted images of each participant were coregistered to the mean of the resliced functional data. T1 was then segmented and spatial normalization parameters were obtained. The deformation parameters were applied to the realigned and unwarped functionals images, which were then spatially smoothed with 3D Gaussian filter with FWHM = 8 mm.

2.2.4. Statistical analyses

Analyses of neuropsychological measures were conducted using two sample *t*-tests in R-Studio (http://www.r-project.org/). To assess the influence of different semantic factors at trial level in CCT on response times (RTs), we implemented generalized linear mixed effects models between and within-groups using Lm4 package (Bates et al., 2015). Three factors were examined: (1) easiness understanding probe-target relationships; (2) frequency of probe-target co-occurrence; (3) difficulty rejecting distractors. Deviation code was used for the categorical predictor (i.e., age group) and continuous semantic predictors were standardized (i.e., CCT's factors) to avoid multicollinearity issues (Barr et al., 2013).

The analyses of RT data collected during scanning and post-scanning accuracy in the object naming task were conducted by including age group (young, older) as between-subject factor and typicality (atypical, typical) as a within-subject factor using generalized linear mixed effects models. RT data of one older participant was missing due to corrupted E-Prime file.

All data collected under the neuropsychological assessment and the experimental task, as well as the R code used in the present study are available at github: https://github.com/maraalves/Typicality-ageing-fmri.git.

Statistical analyses of the fMRI data were performed using the interface in SPM12 (https://www.fil.ion.ucl.ac.uk/spm/doc/) to generate statistical maps in two-levels. At the first level, within-subject data were modelled in two ways. One model included a naming factor for all items as the regressor of interest along with six nuisance regressors for the motion parameters. Another model included a binary typicality factor for typical and atypical items along with six motion parameters introduced as nuisance regressors. In both models, data were locked to the onset of the trials and included the full trial duration (i.e., 3500 ms). Data were modelled using the canonical hemodynamic response function (HRF). In the second level, individual maps contrasting experimental conditions and the implicit baseline (i.e., rest) were included in a between-group random effects model analysed by two-sample *t*-tests. Global measures of grey and white matter volumes were included in the model as covariates to regress out the effects of these brain parameters known to decline with age (Kennedy and Raz, 2009; Raz et al., 2005). In our study, the age groups differed significantly in grey matter volume (t (26.67) = 6.79, $p < .001$), but not in white matter volume (t (23.46) = 0.742, $p = .465$; see Table 1), even though there was a significant and positive association between grey and white matter volumes for older adults ($r = 0.427$, $p = .021$).

We then tested: (1) main effects of naming (i.e., activation during object naming against the baseline, combining young and older adults); (2) main effects of typicality (atypical > typical objects; atypical < typical objects; i.e., greater activation for atypical vs. typical objects, across the young and older groups); (3) main effects of age (older > young; older < young; i.e., over- or under-activation of older relative to young adults in the naming task); and (4) interaction between age group and typicality. Results were thresholded at $p < .001$ uncorrected at voxel level and only clusters that survived $p < .05$ FWE (family-wise error) corrected for multiple comparisons across the entire brain were considered significant. All coordinates reported are in MNI space. The MRIcron package was used for visualizing the brain images (Rorden et al., 2007). The third version of the automated anatomical atlas (AAL3; http://www.oxcns.org/) was used for anatomical notation. This atlas comprises multiple parcellations of orbitofrontal cortex, anterior cingulate cortex and thalamus, by adding new subdivisions according to recent updates (Rolls et al., 2015, Rolls et al., 2020).

3. Results

3.1. Neuropsychological assessment

Mean score in MoCA test was 25.93 ($SD = 2.49$) for older adults, and 27.14 ($SD = 1.99$) for young adults, with no significant difference between groups (t (26.41) = 1.45, $p = .160$), as shown in Table 1. The inspection of scores by domain revealed that older adults presented well-preserved abilities, with both groups scoring high to very high in all domains, except in the memory index, in which performance for older adults ($M = 10.20$, $SD = 4.02$) was significantly lower than young adults' performance ($M = 12.79$, $SD = 2.01$; t (20.87) = 2.21, $p = .038$). This suggests that episodic abilities, loading the memory index (Julayanont el al., 2014), were diminished in older relative to young participants, a well-known marker of cognitive ageing (Park and Reuter-Lorenz, 2009; Salthouse, 2004, 2019; Verhaeghen, 2003). In the attention index (total 18), despite the high scores across groups, we found a tendency for older adults ($M = 17.27$, $SD = 1.03$) to score lower than young counterparts ($M = 17.86$, $SD = 0.36$; t (17.62) = 2.08, $p = .052$). The attention index is loaded in working memory capacity, which is also known to decline along ageing (Park et al., 2002).

Verbal semantic capacity was high and equivalent between groups (t (26.56) = −0.382, $p = .705$), with both young ($M = 15.86$, $SD = 1.74$) and older participants ($M = 16.13$, $SD = 2.14$; see Table 1) scoring above the standardized mean in the vocabulary subtest of WAIS. The ability to visually inspect images to select appropriate features linking probe-target items, while avoiding irrelevant associations with distractors, was also preserved in both groups, with young ($M = 0.89$, $SD = 0.07$) and older participants ($M = 0.89$, $SD = 0.08$) scoring high in the picture version of CCT. No significant difference in accuracy was found between groups (t (26.30) = −0.176, $p = .862$), although there was a significant

difference in the time to respond, with older participants ($M = 7425$, $SD = 2404$) being slower than young participants ($M = 3325$, $SD = 750$; $t(16.88) = 6.29$, $p < .001$). The overall slowdown is also a common element of ageing (Salthouse, 1996, 2019). Further analyses at trial level (Table 3) showed a significant and negative effect of Factor 1 ($B = -1142$, $SE = 381$, $p = .003$), indicating greater facilitation in selecting the target when the feature shared with the probe was easier to identify. The effect of Factor 2 was also significant and negative ($B = -234$, $SE = 94.3$, $p = .013$), suggesting shorter RTs as the co-occurrence between probe and target items increased. The effect of Factor 3 was significant but positive ($B = 637.9$, $SE = 289.5$, $p = .028$), thus indicating longer RTs as the semantic competition of distracter items increases. A significant interaction was found only between age group and Factor 3 ($B = -1220$, $SE = 425.5$, $p = .004$). The nature of this interaction was further investigated by analysing each group separately. Results in young adults confirmed the negative effect of both Factor 1 ($B = -835$, $SE = 285$, $p = .004$) and Factor 2 ($B = -163$, $SE = 71.5$, $p = .022$), but no significant effect of Factor 3 ($B = 36.8$, $SE = 219$, $p = .867$). For older adults, no significant effect of Factor 1 was observed ($B = -1000$, $SE = 860$, $p = .245$), although the effect of Factor 2 was confirmed significant and negative ($B = -458$, $SE = 200$, $p = .022$), suggesting no difference when the relationship between probe and target items was easier to understand, but a reduction on RTs when the co-occurrence between probe and target increased. For Factor 3, however, there was a significant and positive effect ($B = 2490$, $SE = 646$, $p < .001$), suggesting longer RTs as the semantic competition increased in older ages.

3.2. Behavioural performance

RTs in the object naming task carried out during scanning, and accuracy in the task conducted post-scanning are shown in Table 4. Data were analysed by implementing an ANOVA with age-group as between-subject factor and typical and atypical objects as within-subject factor. It is worth noting that in the fMRI naming task, RTs were a crude measure of performance, as participants had to silently name each object and then press a button once the object had been identified. Despite this constrain, we found a significant typicality effect ($B = -35.8$, $SE = 9.6$, $p < .001$), with longer RTs for atypical ($M = 1377$ ms, $SD = 32$) than typical objects ($M = 1305$ ms, $SD = 31$). There was no significant difference between age groups ($B = 7.63$, $SE = 60.2$, $p = .900$) nor a significant interaction between group and item typicality ($B = 10.52$, $SE = 9.6$, $p = .281$). Post-scanning accuracy was overall very high in both groups (young: $M = 0.92$, $SD = 0.04$; old: $M = 0.90$, $SD = 0.05$), and no significant effects were found (Typicality: $B = 0.2$, $SE = 0.46$, $p = .596$; Age Group: $B = 1.0$, $SE = 0.83$, $p = .231$; Typicality x Age Group: $B = -0.56$, $SE = 0.46$, $p = .224$, indicating that both typical and atypical objects were easily recognized by young and older participants.

Table 3
Estimates of fixed effects in the generalized linear mixed effect model for RT in the CCT for young and older adults.

	RT [ms]		
	B (*SE*)	*t*	*P*
Fixed			
Group	−3828.1 (352.9)	−10.85	<.001
Factor 1	−1142.9 (381.3)	−2.99	.003
Factor 2	−234.6 (94.3)	−2.49	.013
Factor 3	637.9 (289.5)	2.20	.028
Group:Factor 1	697.3 (586.8)	1.19	.235
Group:Factor 2	146.8 (139.3)	1.05	.292
Group:Factor 3	−1220.6 (425.5)	−2.87	.004
	σ^2	*SD*	
Random			
Trial	147921.39	384.61	
Subject	713021.72	844.41	

Table 4
Mean performance (standard deviation) on the object naming task for young and older participants.

	Young	Older
RTs [ms, scanning]		
Atypical	1374 (36)	1380 (300)
Typical	1323 (37)	1287 (240)
Accuracy [post-scanning]		
Atypical	.92 (.05)	.89 (.07)
Typical	.92 (.04)	.91 (.05)

3.3. fMRI results

We first inspected brain regions underlying object naming against the baseline in both age groups, as shown in Table 5 and Fig. 1. As reported in previous meta-analyses (Chouinard and Goodale, 2010; Joseph, 2001; Price et al., 2005), object naming was associated with an extensive neural network, including visual areas in bilateral inferior occipital gyrus (BA 19), left fusiform gyrus (BA 19, 37) and right inferior temporal gyrus (BA 37). Activation was also found in left thalamus, left putamen (BA 48), supplementary motor area (SMA; BA 6), right precentral gyrus (BA 6) and right anterior cingulate gyrus (BA 24).

To investigate typicality effects, we contrasted activation between typical and atypical objects in both age groups. Significantly greater activation was found for atypical compared to typical objects (atypical > typical), in left SMA (BA 6; see Table 6). No significant greater activation was found for typical relative to atypical items (typical > atypical), not even at a lower threshold ($p < .005$, 20 voxels).

Age-related changes found by contrasting activity in old and young adults in naming all items against the baseline are presented in Table 6 and Fig. 2. Underactivation for older relative to young adults (old < young) was found in the bilateral posterior regions of the superior temporal gyrus (BA 22), left insula (BA 48), left pallidum, left putamen and left SMA (BA 6). No significant overactivation was found for older relative to young (older > young), not even at a lower threshold ($p < .005$, 20 voxels).

An interaction between age group and object typicality was found in several regions, as shown in Table 7 and Fig. 3, including the left hippocampus (BA 36), extending to fusiform gyrus (BA 20) and middle temporal pole (BA 20); left calcarine (BA 18, 17) and inferior occipital cortex (BA 18); left medial orbitofrontal gyrus (BA 10/11) and anterior cingulate. As anterior portions of temporal lobes have been implicated in the processing of more atypical concepts, contrasts estimate for typical and atypical concepts were taken from the peak MNI coordinate at left temporal pole (−48 12–37 mm; see Fig. 2A; see also Fig. A.1 of the

Table 5
Brain regions demonstrating significant increases of response for object naming (minus rest) across age groups.

Regions	BA	KE	Z	MNI coordinates [mm]		
				X	Y	Z
Object naming > rest						
R inferior temporal gyrus	37	2862	5.58	42	−54	−10
R inferior occipital gyrus	19		5.55	44	−68	−19
R inferior occipital gyrus	19		5.40	42	−80	−4
L inferior occipital gyrus	19	2154	6.03	−44	−78	−4
L fusiform gyrus	19		5.90	−24	−62	−13
L fusiform gyrus	37		5.72	−34	−60	−13
R precentral gyrus	6	1433	4.66	24	−22	44
L supplementary motor area	6		4.61	−6	0	53
R anterior cingulate gyrus	24		4.61	2	−2	32
L thalamus	–	179	4.95	−10	−18	5
L thalamus	–		4.39	−22	−22	8
L putamen	48		4.20	−30	−16	2

Note. BA = Brodmann area, KE = Cluster extent size, Z = Z-Statistic score, L = Left hemisphere, R = Right hemisphere.

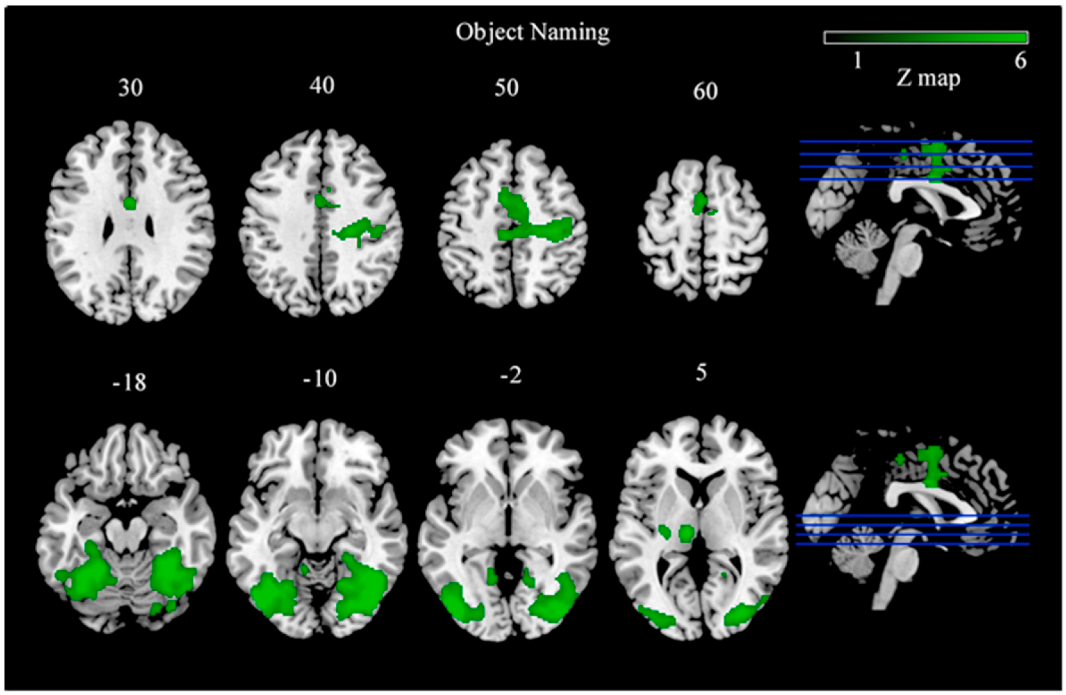

Fig. 1. Brain regions showing significant activation for naming objects (typical and atypical) across both age groups (young and old). Z-stat map, p < .001 uncorrected at voxel level and p < .05 FWE at cluster level. Representative axial slices are presented, with the respective MNI Z coordinate [mm] shown on top.

Table 6
Brain regions demonstrating significant increases of response during naming of atypical vs. typical objects and for young vs. older adults.

Regions	BA	KE	Z	MNI coordinates [mm]		
				X	Y	Z
Atypical > Typical						
L supplementary motor area	6	142	3.77	−2	0	56
L supplementary motor area	6		3.24	−6	14	56
Older < Young						
L superior temporal gyrus	22	556	4.65	−56	−24	8
L superior temporal gyrus	41		4.46	−48	−40	17
L superior temporal gyrus	22		4.32	−62	−30	11
L insula	48	188	4.00	−38	12	−4
L pallidum	–		3.95	−26	−8	−1
L putamen	–		3.95	−24	4	−1
L supplementary motor area	6	182	4.21	−8	0	53
R middle cingulate gyrus	24		4.25	4	2	47
R superior temporal gyrus	22	152	4.03	60	−20	8
R superior temporal gyrus	22		3.82	55	−16	5

Note. BA = Brodmann area, KE = Cluster extent size, Z = Z-Statistic score, L = Left hemisphere, R = Right hemisphere.

Appendix for contrast estimates of all cluster coordinates presented in Table 7). The left temporal pole was deactivated in both age groups (Fig. 2B). While older adults exhibited less deactivation in atypical relative to typical objects, young participants presented less deactivation for typical in comparison to atypical objects, resulting in the significant interaction.

We then investigated typicality effects for each age group separately (see Table 8, Fig. 4). For young adults, activations associated with naming typical relative to atypical objects were found in left calcarine (BA 17) and bilateral lingual gyrus (BA 18); IFG pars triangularis (BA 45), extending to middle frontal gyrus (BA 46) and IFG pars orbitalis (BA 47); pars opercularis (BA 44), extending to precentral gyrus (BA 6). The reverse contrast (atypical > typical) did not demonstrate significant clusters (even at a lower threshold). For older adults, the contrast of typical minus atypical did not show significant clusters (not even at $p <$ .005, 20 voxels). Naming atypical vs. typical objects revealed significant activations in left medial orbitofrontal gyrus (mOFG; BA 10, 11), as well as in left hippocampus (BA 36; extending to left temporal pole at $p <$ .005, 20 voxels).

4. Discussion

This study aimed to investigate how neurocognitive changes in healthy ageing modulate naming of typical and atypical objects. We built upon evidence suggesting that semantic representation and control mechanisms rely on distinct brain regions, which are differentially affected by age. Our results showed that different brain regions adapt from young to older ages to support naming abilities of objects varying in concept typicality.

4.1. Age-related differences in semantic representation regions

We found a significant interaction between age group and typicality in the left polar area of middle temporal lobe (BA 20), reflecting greater activation of this region for older adults during naming of atypical (compared with typical) items relative to young participants (for the inverse contrast). The involvement of anterior portions of the left temporal lobe in naming atypical objects in healthy older adults corroborates extensive evidence for the role of this region in processing conceptual structures of less interrelated features in SD patients across tasks (e.g., Lambon-Ralph et al., 2009; Rogers et al., 2015; Woollams, 2012; Woollams et al., 2008), and extends these findings to healthy ageing. There is compelling evidence for richer and more diverse semantic repositories throughout the lifespan (Hoffman, 2018; Park and Reuter-Lorenz, 2009; Salthouse, 2004, 2019; Verhaeghen, 2003), which promotes older adults' greater accuracy in categorizing atypical items compared to younger participants (Alves et al., 2021). The present results are in line with these findings, by showing that the ATL is significantly more recruited by older than young participants during naming of atypical objects (relative to typical ones). Furthermore, this greater recruitment of ATL for atypical objects is consistent with the idea that the structure of these concepts despite enriched in older ages, remains

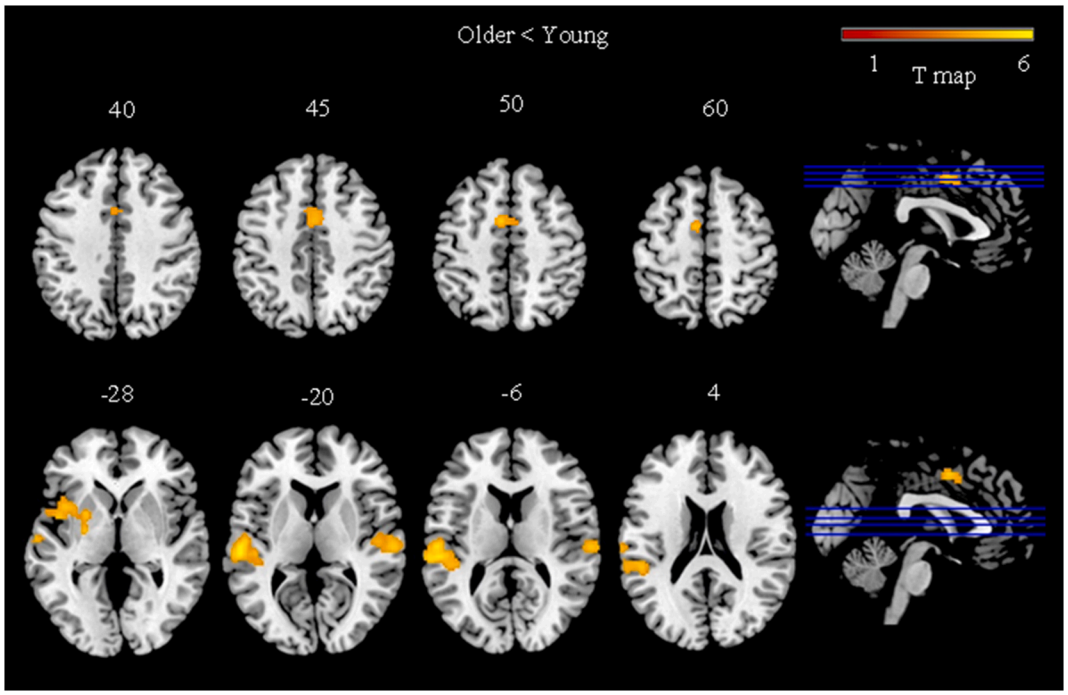

Fig. 2. Brain regions showing significant underactivation for older relative to young adults in naming objects (typical and Atypical). Z-stat map, $p < .001$ uncorrected at voxel level and $p < .05$ FWE at cluster level. Representative axial slices are presented, with the respective MNI Z coordinate [mm] shown on top.

Table 7
Regions demonstrating a significant age by typicality interaction.

Regions	BA	KE	Z	MNI coordinates [mm]		
				X	Y	Z
L medial orbitofrontal gyrus	10/11	237	4.30	−10	60	−7
anterior cingulate gyrus	–		4.21	0	40	2
L medial orbitofrontal gyrus	10		4.12	−6	52	−1
L calcarine gyrus	18	175	4.50	−14	−94	−4
R inferior occipital gyrus	18		4.19	22	−90	−1
L calcarine gyrus	17		3.92	0	−94	−4
L Hippocampus	36	147	4.45	−24	−10	−25
L middle temporal pole	20		4.19	−48	12	−37
L fusiform gyrus	20		3.92	−34	−6	−28

Note. BA = Brodmann area, KE = Cluster extent size, Z = Z-Statistic score, L = Left hemisphere, R = Right hemisphere.

less strongly represented, at least when compared to more typical concepts. Recent behavioural studies analysing the connectivity of semantic networks across age groups have shown that words less well integrated in younger ages increase progressively their associations until midlife (Dubossarsky et al., 2017), although in later ages this pattern is reversed by a decrease in word connections (Dubossarsky et al., 2017; Wulff et al., 2018). This suggests that increments of knowledge (increasing number of words) in late adulthood is crisscrossed by weakened connections sustaining the link between semantic representations (Wulff et al., 2019). This ageing of semantic integration processes may maintain at a lower level the representation strength for more atypical concepts due to weak links between the increasing number of features, thus eliciting additional resources in older adults to select and retrieve information related to those concepts.

For older adults, the contrast of atypical minus typical also recruited activation in hippocampus (BA 36) at left MTL. The recruitment of closely located areas, notably the perirhinal cortex (BA 35, 36), has been reported in tasks requiring the individuation of objects using their specific names, but not when the identification of the higher-order category is required (Moss et al., 2005; Taylor et al., 2007). This suggests that the role played by regions within the MTL in the discrimination of objects and resolution of ambiguity induced by feature similarity (Clarke and Tyler, 2015; Moss et al., 2005; Tyler et al., 2004a, Tyler et al., 2004b, Tyler et al., 2013; Wright et al., 2015) assumes preponderance also in the individuation of more atypical than typical objects in older ages. This indicates that over the lifespan the representation of atypical concepts may be enriched by category-related features, increasing the similarity with other category members (Alves et al., 2021; Rogers and McClelland, 2004). Neuropsychological evidence have already demonstrated that rehabilitation programs offer greater efficacy when focused on the feature complexity of atypical concepts (Gilmore et al., 2020; Kiran and Johnson, 2008; Kiran et al., 2007, 2011; Kiran and Thompson, 2003; Sandberg et al., 2012; Stanczak et al., 2006). Moreover, Cutler et al. (2019) have showed that patients with hippocampal damage produced fewer features (indexed by vectors in the semantic space), and the generated features were more closely related to the concepts prompted compared to healthy older controls who not only generated more features, but also produced features more distal to the targeted concept in the semantic space. These results highlight the role of the hippocampus in conceptual representation, and the tight connection between semantic and episodic memory systems (Duff et al., 2020).

Furthermore, these findings highlight the importance of further understanding the dynamics between anteromedial and anterolateral regions of temporal lobes in the semantic processing along ageing. Thus far, it is thought that both regions provide streams of feedback to more posterior visual areas to support fine-grained object-identification (Clarke et al., 2018), possibly expressing the similarity structure of concepts (Martin et al., 2018). Such processing seems to be particularly relevant as age increases, potentially to adapt changes in the reorganization of semantic structures (Dubossarsky et al., 2017; Wulff et al., 2018, 2019) and/or overcome the decline in neural responsivity affecting visual and conceptual processing (Bruffaerts et al., 2019; Samu et al., 2017).

It is noteworthy that, as in other fMRI studies (e.g., Baciu et al., 2016; Berlingeri et al., 2010; Ferré et al., 2020; Hoyau et al., 2018; Lacombe et al., 2015), older and young participants presented equivalent semantic performance in the current naming task. The same was observed for retrieving word definitions without time constrains in the vocabulary

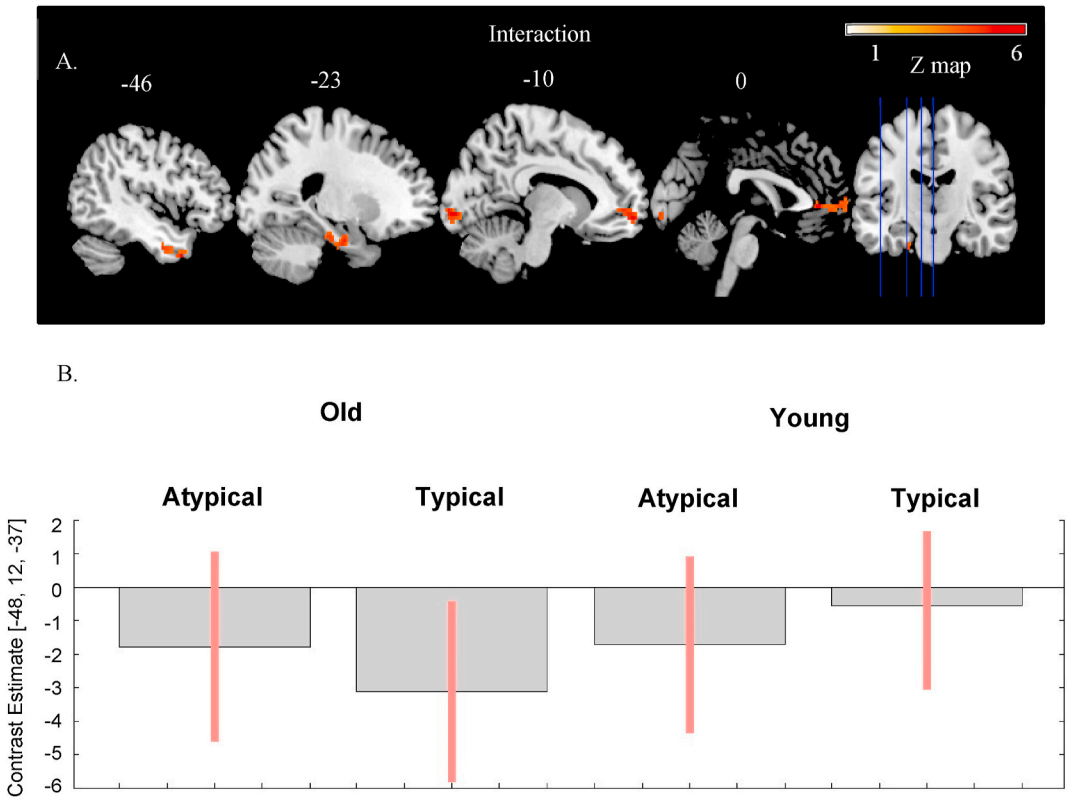

Fig. 3. A. Brain regions showing significant interaction between age and typicality. Z map, $p < .001$ uncorrected at voxel level and $p < .05$ FWE at cluster level. Representative sagittal slices are presented, with the respective MNI X coordinates [mm] show on top; B. contrasts estimate for naming typical and atypical objects (minus rest) for each age group (old, young) and 90% confidence intervals (C.I.) for the MNI coordinate at middle temporal pole (−48, 12, −37) mm.

Table 8
Regions demonstrating significant activation during naming of typical and atypical objects in young and older participants.

Regions	BA	KE	Z	MNI coordinates		
				X	Y	Z
Young Adults Typical > Atypical						
L calcarine	17	507	4.31	−14	−98	−1
R lingual	18		4.00	18	−90	−13
R lingual	18		3.77	14	−84	−4
L IFG *pars triangularis*	45	233	3.89	−48	40	2
L middle frontal gyrus	46		3.77	−42	48	2
L IFG *pars orbitalis*	47		3.72	−40	42	−7
L IFG *pars opercularis*	44	140	3.96	−42	18	35
L precentral gyrus	6		3.80	−46	6	38
L middle frontal gyrus	46		3.68	−48	28	32
Older Adults						
Atypical > Typical						
L anterior cingulate gyrus	10	355	4.65	−4	50	−1
L medial orbitofrontal gyrus	11		4.56	−10	60	−7
R anterior cingulate gyrus	–		4.48	2	40	2
L hippocampus	36	128	5.01	−24	−10	−25
L cerebellum	37		4.02	−34	−60	−28
L parahippocampal gyrus	30		3.76	−22	−22	−25

Note. BA = Brodmann area, KE = Cluster extent size, Z = Z-Statistic score, L = Left hemisphere, R = Right hemisphere.

WAIS subtest, and in inspecting images to identify the appropriate features linking probe-target items in the CCT. This lack of group differences and the overall high performance of both groups across all semantic tasks confirms that semantic processing was preserved in the elderly. In the CCT, however, we found a significant difference in RTs between groups. This effect was qualified by an interaction between age and semantic control in the analysis examining the influence of distinct semantic mechanisms at trial level. Specifically, longer time-latencies in older adults, but not in young participants, were observed only when correct responses were selected among strong semantic competitors. In main naming task, however, older participants not only matched young participants in terms of accuracy but also exhibited similar RTs, with both age groups presenting longer RTs for atypical relative to typical items. One possible explanation is that older adults may offset cognitive decline in semantic control by taking advantage of their enlarged semantic repositories to uphold successful performance at the level of younger ages (Hedden et al., 2005; Hoffman and Morcom, 2018). Such compensatory strategy would explain equivalent performance in the naming task, in which older adults may have used their enriched knowledge to respond as accurately as possible within the controlled response-time limits.

4.2. Age-related differences in semantic control regions

Accessing the specific name for atypical, relative to typical objects, elicited activation of the medial orbitofrontal gyrus in older relative to young adults, as reflected by the significant interaction. Activity in this prefrontal region, adjacent to the IFG, has not been reported in meta-analyses of object identification with young adults (e.g., Chouinard and Goodale, 2010; Joseph, 2001; Price et al., 2005) nor in ageing studies using naming tasks (e.g., Baciu et al., 2016; Berlingeri et al., 2010, 2013). Of note, it has been associated to patterns of neuroanatomical enlargement along ageing (Salat et al., 2004), which contrasts to the decline observed in other prefrontal regions (Kennedy and Raz, 2009; Nordahl et al., 2006; Raz et al., 2005). Hence, this constitutes a potential neural resource for a compensatory mechanism (Cabeza et al., 2018; Gutchess et al., 2007). The involvement of the orbitofrontal cortex in top-down processes of object identification has been discussed in

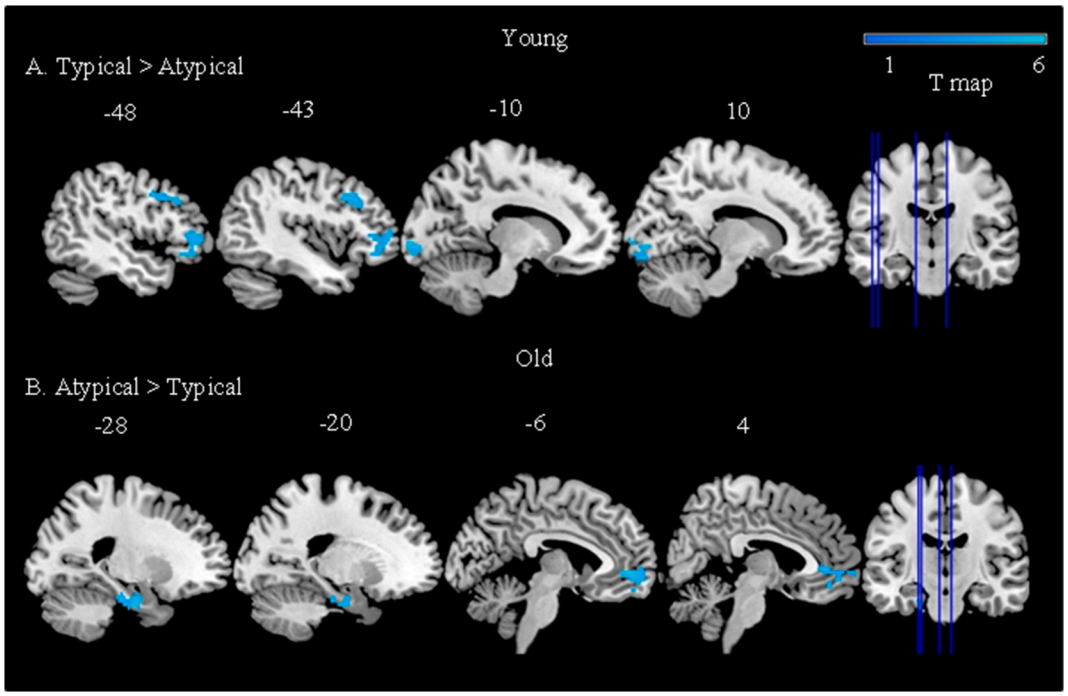

Fig. 4. A. Brain regions activated for typical minus atypical in young adults; B. Brain regions activated for atypical minus typical older adults. T maps, $p < .001$ uncorrected at voxel level and $p < .05$ FWE at cluster level in all cases. Representative sagittal slices are presented, with the respective MNI Z coordinate shown on top.

comparison to other prefrontal regions. For instance, while the IFG has been systematically linked to the retrieval and selection of information from memory (Badre and Wagner, 2002, 2007; Bar, 2003; Thompson-Schill et al., 1997), the orbitofrontal gyrus may have instead a regulatory role of performance (Bar, 2003, 2007; Ridderinkhof et al., 2004a; 2004b). After activation of stimulus-specific information at perirhinal areas, it is thought that this region plays a role in adjusting and directing back predictions only on the objects relevant features to support the appropriate behaviour according to the task demands (Bar, 2003, 2007).

Moreover, there was no evidence of a typicality effect at IFG for older participants. Instead, the presumed reorganization of semantic connectivity (Dubossarsky et al., 2017; Wulff et al., 2018, 2019) and/or the potential decline of neural responsivity in areas activated in younger adults (Bruffaerts et al., 2019; Hoffman and Morcom, 2018) seems to have elicited greater prefrontal control demands, particularly for more atypical concepts, possibly involving monitoring processes located at mOFG to redirect processing after adjusting predictions based on prior object information (Bar, 2003, 2007; Ridderinkhof et al., 2004a; 2004b). Interestingly, along with the top-down role of orbitofrontal areas, there is evidence of ATL as a crucial component in modulating semantic processing. For instance, after inhibitory stimulation at ATL, Chiou and Lambon-Ralph (2016) reported a typicality effect in naming, benefiting more typical items, only in situations of reduced bottom-up visual information (up to 40 ms of stimuli exposition). This suggests that representations of most usual object feature configurations may be advanced as predictions, with more typical objects matching the expected representations sooner them more atypical objects (Chiou and Lambon-Ralph, 2016).

In our study, activation of the left IFG was found only for young adults specifically in naming typical relative to atypical objects. This suggests that in younger ages the access to the specific names of typical objects is more demanding than naming atypical objects, recruiting more semantic control processes. This finding contrasts to the study of Santi et al. (2016), in which activity in this brain region was reported during the categorization of more atypical items in younger adults. Importantly, the parametric modulation of typicality values in this previous study differs from our binary manipulation (i.e., typical vs atypical items), although this does not explain the reverse pattern of the typicality in the IFG. Instead, there is compelling evidence suggesting that naming and categorizing objects pose different control demands. Presumably, semantic control is differently engaged in the processing of typical and atypical objects depending on whether the task requires the assessment of concepts feature sharedness patterns for categorization purposes, or the individuation of objects by accessing their specific names. Consistent with this view, Rogers et al. (2015) have showed that disrupted control abilities in SA patients produced variant typicality effects across naming and categorization tasks. Such neuropsychological findings contributed to reify the controlled semantic cognition account, in which the interactive dynamics between semantic control and representation aspects of cognition consider the nature of concepts structured over feature similarity (Jefferies, 2013; Jefferies et al., 2020; Lambon-Ralph, 2014; Lambon-Ralph et al., 2017; Rogers et al., 2015). Here we present evidence suggesting that, in younger ages, semantic control processes in IFG were recruited during naming of typical objects probably due the amount of competition posed by similar objects within the same category.

In pMTG, however, we found a pattern of underactivation for older adults relative to younger counterparts across all items. Such result may indicate that naming in later stages of life is overall less demanding on the semantic control resources allocated to this region (see Jefferies, 2013; Jefferies et al., 2020). It is also possible that such underactivation may result from a generalized decrease in BOLD signal-to-noise ratio due to the natural decline of neurobiological structures over time (Gazzaley & D'Esposito, 2005). Despite this inherent aspect in neuroimaging studies comparing young and older adults, with structural- and arterial-dependent measures offering alternatives to regress out ageing effects (Rugg & Morcom, 2005), it is important to note that in our study, like in many others, we observed patterns of overactivation for older adults (Cabeza e t al., 2005; Hoffman and Morcom, 2018). In a meta-analysis, Hoffman and Morcom (2018) also demonstrated that older adults showed particularly less activation in both left IFG and left

pMTG, although for the later the age-related difference was only significant when older adults performed more poorly than younger adults. Of note, the pattern found in pMTG differs from the one found in IFG, thus suggesting that these two regions play distinct roles in semantic processing. The absence of typicality effects suggests that, at least for covert naming, activity at pMTG is not modulated by the distinct demands in naming objects varying in concept typicality.

4.3. Caveats and future studies

Neuroimaging studies comparing young and older participants have shed light on the multifactorial changes occurring from structural to cognitive domains along the lifespan (Cabeza et al., 2005; 2018; Raz et al., 2005). The age groups in the current study presented comparable semantic performance and brain volume differences were regressed out in fMRI analyses. Yet, the sampling of the two groups comprised different age ranges, and included highly educated individuals, entangling possible cohort effects (Raz et al., 2005). The reduced sample size and the relatively small number of stimuli used in this study warrant some caution in the interpretation of the results as they may not provide a complete picture of the age-related typicality effects. Recently, using a large age range sample of adults, Diaz et al. (2022) showed decreasing activation in IFG, parahyppocampal gyrus and MTG, with increasing number of semantic neighbours (indexed to the degree of feature overlap) of objects. Yet, there was no evidence of brain regions showing a positive effect, nor interactions with age. We should also note that the typicality ratings used here were taken from a previous study with young adults (Santi et al., 2016), and it is unclear if and how these ratings change along ageing. On the one hand, increasing knowledge over the lifespan may change typicality ratings specifically for more atypical items, which may be rated as less atypical for older adults compared to younger counterparts. Previous studies provide some evidence in support of this hypothesis by showing increased typicality ratings from infancy to early adulthood (Bjorklund et al., 1983), as well as increased accuracy from young to older ages in categorizing atypical instances (Alves et al., 2021). On the other hand, typicality ratings reflect the structural features of objects, i.e., the degree of feature sharedness/distinctiveness among objects of the same category (Marques and Charnallet, 2013; Rogers and McClelland, 2004). Hence, the differentiation of concepts over learning will capitalize the feature covariation pattern inherent to each concept (Rogers and McClelland, 2004). In this regard, the relationship between typicality judgements and the pattern of feature sharedness may remain linear along adulthood. As such, whether collecting typicality ratings with older adults would significantly change the ratings, and the extent to which this would impact neural activity are open questions that this study was not designed to address. In future studies, it will be relevant to validate typicality ratings in independent samples of older adults, and then test for negative and positive typicality and age effects in distinct brain regions in larger and more representative samples of participants.

Also, inside the scanner our naming task was covert, i.e., did not involve the verbal naming of objects. This poses two concerns. First, covert naming may minimise post-semantic processes such as the access to phonological lexicon and additional processes of word production (Levelt et al., 1999; Oppenheim et al., 2010) known to be affected by tip-of-the-tongue effects in older ages (Bruffaerts et al., 2019; Shafto and Tyler, 2014; Wulff et al., 2018, 2019). Such effects were residual in our study, which in part may be due to the fact that overt naming only occurred after the scanning task, with the repeated presentation of the objects. Second, RTs collected inside the scanner were a crude measure of naming abilities, as button-press occurred after silent naming. In future studies, it will be important to circumvent these limitations by using an overt naming task (e.g., combined with sparse-imaging acquisition) to ensure that accuracy and RTs are more reliable measures of naming abilities. Also, the combined use of fMRI and other neuroimaging methods with good time-resolution, such as electroencephalography (EEG), may be key to clarify whether and when brain regions, like the IFG, are engaged and reach the threshold beyond which activation declines thus indicating the limit of neural resources, and then unlock the involvement of additional brain regions.

4.4. Conclusion

The involvement of anterior portions of temporal lobe in processing more atypical concepts in healthy older adults converges to the proposal that holds this region as a semantic representation hub extracting feature similarity structures (e.g., Lambon-Ralph et al., 2017). Its overactivation in older ages supports the view that enriched semantic repositories over time (Alves et al., 2021; Hoffman, 2018) may reorganize functional activity in the ageing brain (Hoffman and Morcom, 2018). On the other hand, the recruitment of left IFG in young adults in naming more typical objects emphasises the key role of control processes and their dynamic interplay with representation mechanisms to approach semantic cognition (Rogers et al., 2015). The greater involvement of top-down processes in orbitofrontal regions in older adults may comprise a successful compensatory strategy (Cabeza et al., 2018) to support the processing of more atypical objects along ageing.

Credit author statement

Mara Alves:Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration Funding acquisition.Patrícia Figueiredo: Methodology, Validation, Writing – review & editing, Supervision, Funding acquisition. Ana Raposo: Conceptualization, Methodology, Validation, Writing – review & editing, Supervision, Funding acquisition.

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Declaration of competing interest

None.

Data availability

Github.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2023.108545.

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