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Semantic memory space becomes denser with age

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ABSTRACT

Semantic memory, a repository for concepts and factual information, plays a vital role in acquiring and retrieving knowledge. This study explores the impact of age-related knowledge accumulation on semantic cognition, investigating whether a denser representational space affects retrieval processes. Using a semantic feature verification task, we employ both behavioral (reaction time; RT) and neurophysiological (event-related potential; ERP) measures to explore these dynamics across young and older adults. Findings revealed an age-related RT difference in retrieval of semantically incongruent features, indicative of increased semantic search demands with age. ERP results show attenuated N400 responses in older adults for congruent features, possibly reflecting increased semantic relatedness. The late frontal effect (LFE) shows sustained modulation in older adults, indicative of enhanced post-retrieval monitoring. We propose that this extended search through semantic memory reflects an increase in the number of features to evaluate. These results support the idea that aging leads to a more densely packed semantic space, impacting the speed and dynamics of semantic retrieval.

1. Introduction

Semantic memory serves as a comprehensive storage system for concepts and factual knowledge acquired throughout an individual's lifetime. It plays a pivotal role in our ability to recall and integrate new events and information into existing mental representations, utilizing feature similarity as a crucial organizational principle (Rosch, 1975; Sajin and Connine, 2014; Smith et al., 1974). Semantic memory retrieval can be conceptualized as a search through a vast conceptual landscape, where the congruence between a retrieval cue and sought after target influences the likelihood of successful recall (Raaijmakers and Shiffrin, 1980; Shiffrin and Steyvers, 1997; Thomson and Tulving, 1970). The dynamic interplay between semantic representation and semantic control constitutes semantic cognition - our ability to use, manipulate and generalize knowledge (Ralph et al., 2017). Semantic representation refers to the encoding and storage of conceptual knowledge, while semantic control is the executive process that targets and retrieves that knowledge (Chiou et al., 2018). An outstanding question in our understanding of semantic cognition is whether a greater accumulation of knowledge, as occurs in normal aging, results in an altered semantic search process because the representational space itself is denser with more features.

To investigate this question, we must first model semantic representational space. Early work on semantic memory conceptualized it as a network in which representations are structured hierarchically, with more general concepts at the top and more specific concepts at lower levels (Collins and Quillian, 1969, 1970; Rosch, 1975). An alternative to network structures are feature comparison models (Smith et al., 1974) where words are represented as a collection of binary features (e.g. *birds* have wings, *dogs* do not have wings). The similarity of two concepts can be derived by the amount of overlapping features. Network and feature-based models both describe the interplay between a representational structure and a mechanism by which those representations are accessed but are limited in their ability to explain *how* knowledge is learned. To this end, distributional semantic models explicitly create representational spaces by learning statistical regularities from the environment (Griffiths et al., 2007). They leverage a formal cognitive mechanism to acquire semantic knowledge through repeated episodic experiences (Davis and Yee, 2021; Jones, 2019). Thus, the performance of distributional models is enhanced when they are trained on larger amounts of text (Malandrakis et al., 2013; Sahlgren and Lenci, 2016), mirroring the human experience of accumulating semantic knowledge as we age.

To demonstrate how knowledge accumulation with age might alter the density and associations in semantic space, let's use the example of "pencil". A young person might have fewer representations of a pencil

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than an older adult who will have had more exposure to pencils; different colors and styles and uses across different environments. In this way, with age, a pencil becomes more similar to related concepts, such as artist, sketch or notepad because there is more chance of overlapping features between them (see schematic in Fig. 1 for age differences in semantic space). In the current study, we investigate this idea using a combination of behavioral reaction time (RT) and event-related potential (ERP) measures to assess how a denser semantic space impacts the speed with which semantic features are searched for and evaluated. Younger and older adults performed a semantic feature verification task while EEG activity was recorded. Common nouns (target words) were paired with multi-word features that were either congruent, true features e.g. 'pencil - made of lead', or incongruent e.g. 'pencil - is juicy'. For example, 'pencil - has keys' is considered semantically similar but incongruent because both 'pencil' and 'keys' can be associated with writing tools—pencils are used for writing on paper, while keys are used for typing on a computer. Additionally, we manipulated the semantic similarity of the target-feature pairs according to a distributional model (Pennington et al., 2014), so that high-similarity pairs are more similar than low-similarity. Previous aging studies have manipulated either congruence (Alejandro et al., 2021; Packard et al., 2020), or similarity (Zhuang et al., 2016). However, in this novel study, we implement a design that manipulates both congruence and similarity to better understand the influence, and interaction, of these semantic variables on retrieval from semantic memory in older adults.

Event-related potential (ERP) studies have provided insights into the temporal dynamics of memory search processes. ERP components, such as the N400 and, to an extent, the later-frontal effect (LFE) have been implicated in semantic processing and sustained memory retrieval, respectively (Kutas and Federmeier, 2011; Rugg and Curran, 2007). The N400 is known for its sensitivity to meaningful stimuli and semantic manipulations, making it a valuable tool for investigating how meaning-related information is stored in the brain (Kutas and Federmeier, 2011; Rabovsky and McRae, 2014). Increased semantic similarity decreases N400 amplitude (Frank and Willems, 2017; Kounios and Holcomb, 1992), and recent work found that semantic surprise in an oddball task predicts N400 amplitude in single trials (Lindborg et al., 2023). Prior studies have shown that in sentence comprehension tasks, compared to younger adults, older adults show reduced N400 responses to congruent vs. incongruent words ('he shaved off his mustache and city (vs. beard)'), which are thought to be driven by decreases in older adults' ability to make use of context information e.g. how predictable the final word of a sentence is (Federmeier and Kutas, 2005; Payne and Federmeier, 2018; Tiedt et al., 2020; Wlotko et al., 2012; Wlotko and Federmeier, 2012). We would argue that this reduced ability to use context, and attenuated N400, may result from an age-related increase in the density of semantic space. That is, due to a more densely populated semantic space, the semantic violation effect (city vs. beard) is reduced with age because target words have more nearby associates. An additional component of interest is the late frontal effect (LFE), which has been associated with controlled retrieval processes such as post-retrieval monitoring or additional retrieval attempts (Curran et al., 2001; Donaldson and Rugg, 1999). Importantly, Hayama et al. (2008) found that the LFE is observed in semantic and episodic decisions, suggesting it reflects sustained, generic retrieval monitoring across memory domains. Others have shown that older and younger adults show similar recruitment of post-retrieval monitoring processes and the LFE (Horne et al., 2020).

If the process of aging leads to an accumulation of semantic knowledge and a denser semantic feature space, we predict that older adults will be slower than younger adults in one particular condition - rejecting highly similar but incongruent features (pencil - *has keys*). The excellent temporal resolution of ERPs allows us to test the hypothesis that due to a more densely populated semantic space, older adults will exhibit a smaller reduction in N400 amplitude when processing semantically similar features compared to younger adults. This suggests that the N400 effect, which typically decreases with higher semantic similarity, will be less pronounced in older adults. We also expect to find sustained modulation of the LFE in older compared to younger adults when to-be-rejected features have higher feature similarity to targets despite being incongruent. Why do we predict a larger age effect for the feature similarity modulation in the congruent condition for the N400, and for the incongruent condition for the LFE? In congruent trials all features are true but differ in proximity to targets. For older adults, due to a denser semantic space, the effect of semantic similarity on the N400 component will be diminished, indicating a smaller difference in N400 amplitude between high and low similarity features because both high and low congruent features are possible and might have been experienced together before. By contrast for incongruent target-feature pairs, even older adults have not encountered low similarity features associated with a target (pencil - is juicy) and a large semantic violation and N400 modulation by feature similarity should be observed for old and young alike. By contrast, the LFE reflects post-retrieval monitoring that is sustained particularly when decisions are difficult, or require additional evaluation (Cruse and Wilding, 2009). When features need to be rejected (i.e. incongruent condition), those high in similarity to the target word

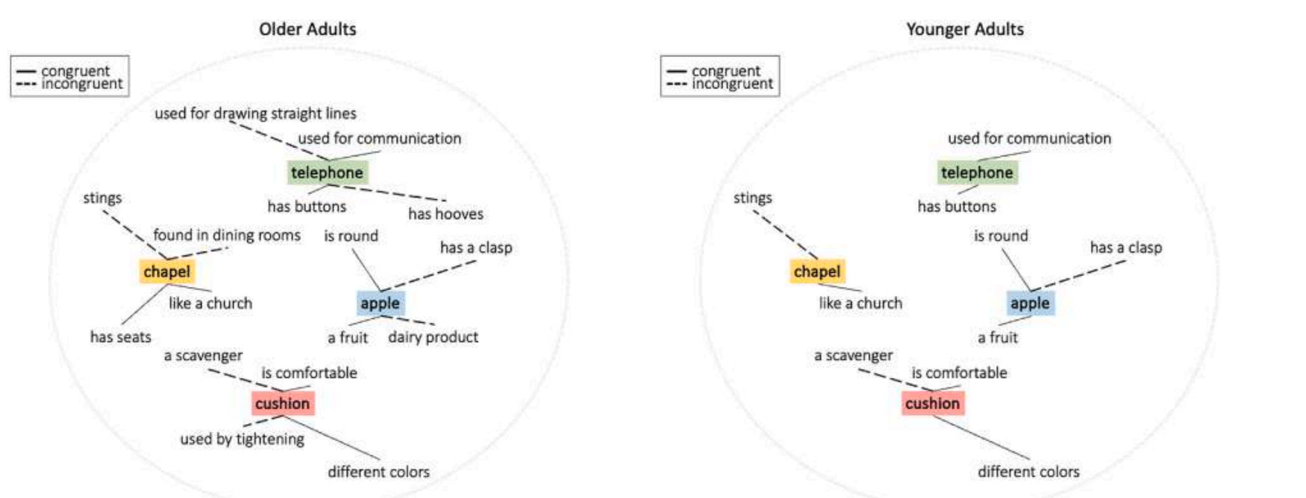

Fig. 1. Schematic of semantic vector space with aging as a model of knowledge accumulation. Older adults (left) have a denser semantic space, including associations between congruent and incongruent target feature pairs. Younger adults (right) have a sparser semantic memory space with less associations, and less competitors during semantic feature retrieval. The length of connections represents cosine distance in semantic vector space.

may require more evaluation than those low in similarity. This would be especially true for older adults if densely populated concepts share more overlapping features because a higher degree of semantic overlap is in conflict with the "no" response that they must produce for incongruent trials. Using age as a model for knowledge acquisition, we test the idea that older adults' semantic memory is more densely packed with conceptual features, impacting the speed and dynamics of semantic retrieval.

2. Materials and methods

2.1. Participants

A total of 60 participants were recruited for the EEG study, divided into two groups: 30 younger adults (18 females, mean age = 21.26, SD = 2.49, age range: 18–28 years, mean years of education = 14.82, SD = 1.42) and 30 older adults (17 females, mean age = 69.5, SD = 5.46, age range: 60–77 years, mean years of education = 16.61, SD = 2.67). All subjects were right-handed, native English speakers and had normal or corrected vision. Participants were recruited from The University of Texas at Austin and the surrounding community, and they were compensated $20/hour. All subjects completed a health questionnaire, and no one reported any psychiatric or neurological disorders. Consent was obtained prior to the experiment in accordance with the UT Austin Institutional Review Board. Older adults completed a standardized cognitive assessment, the Mini-Mental State Examination (MMSE:Molloy et al., 1991), to ensure that group differences were due to healthy aging. All participants scored above 25 (range: 25–30, M = 28.56), the recommended cut-off for cognitive impairment (Crum et al., 1993).

2.2. Stimuli

Target words were 100 common nouns from a dataset of semantic feature production norms (McRae et al., 2005); a set of 541 living and nonliving basic-level concepts. In their study, Mcrae et al. (2005) had 725 participants report up to 30 features for the concepts e.g. moose - '*has antlers*', '*an herbivore*'. We sampled 400 multiword features from the dataset: 200 were true features of a target (congruent), and 200 were randomly selected from other target words (incongruent), but manually confirmed to be unambiguously not a feature. Congruent and incongruent features were evenly split into high and low semantic similarity from the target word. High similarity target-feature pairs had a cosine similarity (1 - cosine distance) greater than or equal to 0.25, and low similarity target-feature pairs had a cosine similarity distance less than or equal to 0.15. These thresholds were set by taking 0.2060, the median cosine similarity of all of the target-feature pairs, and then adding a degree of separation between the high- and low-similarity conditions. This created a 2 × 2 design with 4 conditions: congruent/high similarity, congruent/low similarity, incongruent/high similarity and incongruent/low similarity. See Fig. 2a for an example target word, pencil, with all four stimuli conditions.

2.3. Semantic vector space

To model the organizational structure of semantic memory, we used Global Vectors (GloVe): a semantic vector space model of word representation (Pennington et al., 2014). GloVe is among several computational models that quantifies the meaning of words by allocating each word a position within a high-dimensional vector space (Deerwester et al., 1990; Landauer and Dumais, 1997; Lund and Burgess, 1996; Steyvers et al., 2004). These models use linear algebraic techniques, such as singular value decomposition, to formulate vector representations based on statistical information capturing the co-occurrence patterns of words within large text corpora. Standard distance measures are used to calculate the semantic similarity between words, in the current work we take the cosine angle between the target and feature vectors as

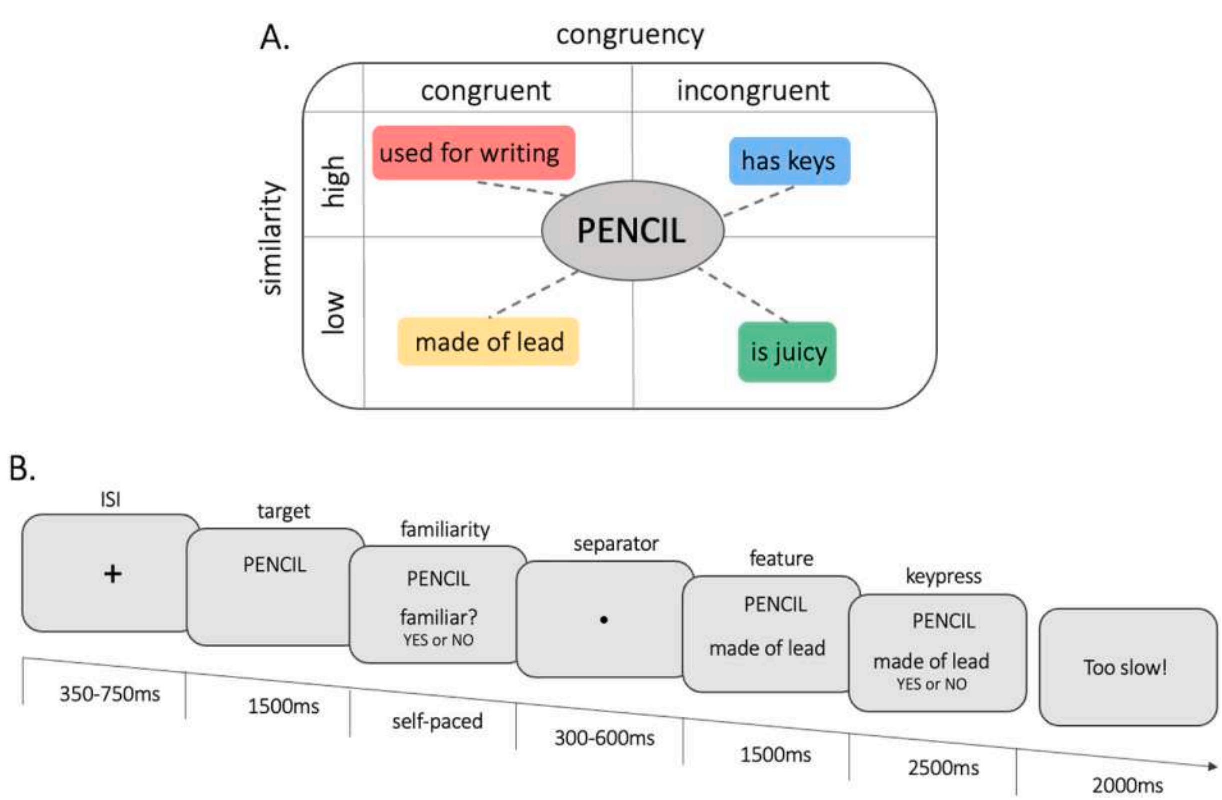

Fig. 2. Schematic illustration of stimuli and trial-level experimental task design. (A) Example stimuli in each condition for target word *pencil*. Features are split by congruency (congruent, incongruent) and semantic similarity (high, low). The congruency of target-feature pairs is independent of their distance in semantic space. Congruent and incongruent features are distributed equally across the space. (B) Time sequence of a single trial.

the cosine distance, and subtract it from 1 to find the cosine similarity, Cos(θ) (Kwantes, 2005). Values of Cos(θ) are bound between −1 (exact opposite) and 1 (identical), and a value of 0 indicates that two words are not meaningfully related. In the current study, we create multi-word feature vectors by averaging the vectors of each of the content words within a feature (Pereira et al., 2018).

2.4. Experimental task

Subjects completed ten practice trials and 400 test trials across four blocks (100 in each block, randomized and evenly sampled from the four conditions). As seen in Fig. 2b, each trial began with a centrally-presented fixation (randomized between 350 and 750ms), followed by the presentation of a target word for 1500ms. We then included a familiarity question to ensure that we were testing memory for known semantic features. Participants responded Yes or No to indicate if they were familiar with the target word or not. If they responded No, that trial ended, and the next one began. If they responded Yes, following another jittered fixation (300–600ms), a multi-word semantic feature was presented below the target word for 1500ms. Participants then had 2500ms to make a keypress response (Yes or No), indicating whether they thought that feature was a true feature of the target word or not. If a keypress was not recorded after 2.5s, a 'too slow!' warning appeared for 2000ms. Participants were instructed as follows: *Please press YES if the feature is commonly considered to be true. For example, you would press YES for "bottle/holds water", even though a bottle can also hold other beverages. Please press NO for features that are highly unlikely or untrue "bottle/made of silk".*

2.5. EEG collection and preprocessing

EEG data were recorded from a 32-channel BrainProducts actiChamp system at 500 Hz sampling rate with 24-bit resolution. The electrodes were placed according to the 10–20 system with Cz channel as the online reference and Fpz as the ground electrode (Jasper, 1958). Electrode positions included: FP1, Fz, F3, F7, FT9, FC5, FC1, C3, T7, TP9, CP5, CP1, Pz, P3, P7, O1, Oz, O2, P4, P8, TP10, CP6, CP2, C4, T8, FT10, FC6, FC2, F4, F8, FP2, O1, Oz, and O2. Two additional electrodes recorded horizontal electrooculogram (HEOG) at the lateral canthi of the left and right eyes and two electrodes placed superior and inferior to the right eye recorded vertical electrooculogram (VEOG).

EEGLAB was used for offline data analysis (Delorme and Makeig, 2004). EEG data was re-referenced to the average of the left and right mastoid electrodes (TP9 and TP10), downsampled to 250 Hz and digitally band-pass filtered between 0.1 Hz and 80 Hz. Continuous data was epoched into time windows from 300ms before, and 1500ms after stimulus feature presentation. Epochs were baseline corrected using the 300ms prior to feature onset. Noisy channels and epochs were rejected based on automated EEGLAB algorithms. Independent component analysis was applied using ICLabel to reject components that were classified as noise from eye movement, muscle or heart with >0.9 probability (Pion-Tonachini et al., 2019).

2.6. Mass univariate ERP analysis

The ERP data was analyzed with a mass univariate permutation test, which allows for correction of multiple comparisons and rigorous control of the family-wise error rate, while remaining statistically powerful (Fields, 2017; Groppe et al., 2011a, 2011b). These cluster permutation analyses offer a sensitive approach for analyzing ERP effects (Maris, 2012; Maris and Oostenveld, 2007). This method recognizes that genuine ERP effects extend beyond individual data points and involve multiple channels activated over multiple time points. The analysis groups neighboring data points in space and time into clusters and calculates the probability of observing these clusters by chance. Importantly, low probabilities for one or more clusters (e.g. $p < 0.05$) don't imply that the activation is localized to specific channels and time points within those clusters. Instead, it suggests differences between conditions (i.e., the data don't share the same probability distribution). The channels and time points of the clusters provide suggestive evidence for the likely location and timing of stimuli-related activation (van Ede and Maris, 2016). Mass Univariate Analysis is designed to control for multiple comparisons across many data points, often focusing on the identification of significant clusters rather than individual effect sizes or CIs. As noted in Groppe et al., (2011c), the focus on permutation-based significance testing within this framework inherently limits the calculation and interpretation of these measures. For this analysis, the ERP data were downsampled to 125 Hz.

2.7. ERP analysis

Following the identification of significant clusters using mass univariate analysis, we conducted separate analyses for the N400 and LFE components. For the N400, we focused on a time window of 350–550 ms post-stimulus at central and parietal electrode sites, which are typically sensitive to semantic processing. The mean amplitude was extracted for each condition, and a 2 × 2 × 2 repeated-measures ANOVA was performed with factors of Age Group (young, old), Congruence (congruent, incongruent), and Similarity (high, low). Similarly, for the LFE, we analyzed data from a later time window (800–1500 ms) at frontal electrode sites, again using repeated-measures ANOVA to examine interactions between these factors. This allows us to explore how age-related changes influence semantic processing at different stages of retrieval.

3. Results

3.1. Behavioral

We first aimed to confirm that our results are based on the congruence and similarity manipulations, and not age-related differences in familiarity with the words that potentially varied by condition. We fit a 2 (Age Group: young, old) x 4 (Condition: congruent/high-similarity, congruent/low-similarity, incongruent/high-similarity, incongruent/low-similarity) ANOVA to the familiarity responses (0 = not familiar, 1 = familiar). There was a main effect of Age Group ($F (1, 220) = 88.37$, $p < 0.001$) due to the fact that older adults showed greater familiarity for the target words than did younger adults (Older: $M = 0.99$, $SD = 0.006$; Younger: $M = 0.97$, $SD = 0.02$). Importantly, there was no effect of Condition and no Age Group × Condition interaction, so subsequent behavioral and ERP results cannot be explained by differences in word familiarity.

Our main behavioral measure was reaction time for the congruency judgment (Yes/No for "*is the feature a true feature of the target word?*"). To analyze the reaction time data, we fitted a generalized linear mixed-effects model (GLMM) using the glmer function from the lme4 package in R (Bates et al., 2015). GLMMs have the benefit of capturing the typical positively skewed reaction time distribution, without needing to transform the data (Lo and Andrews, 2015). The model included reaction time (RT) as the dependent variable and Age Group (2: young, old), Similarity (2: high, low), and Congruity (2: congruent, incongruent) as fixed effects, as well as their interactions. Years of education was included as a covariate because an independent *t*-test revealed that the two age groups significantly differed in years of education ($t (58) = -3.01$, $p = 0.004$). Younger adults (Mean = 14.82 years, SD = 1.42 years) had fewer years of education compared to older adults (Mean = 16.61 years, SD = 2.67 years). A random intercept for subjects was included to account for the repeated measures design. Categorical variables were dummy-coded with "old" (Age Group), "high" (Similarity), and "congruent" (Congruity) as reference levels. Due to the skewness of the RT data, we specified a Gamma family with a log link function. The model was optimized using the 'bobyqa' optimizer to ensure convergence.

We found significant main effects of Congruence (B = 0.3, t (245) = 3.72, p < 0.001) and Similarity (B = 0.03, t (245) = 3.46, p < 0.001). Specifically, participants responded faster to congruent features compared to incongruent features, and faster to high-similarity features compared to low-similarity features (see Fig. 3). There was also a significant interaction between Age Group and Congruence (B = 0.1, t (245) = 5.62, p < 0.001), indicating that older adults experience a more pronounced delay in RT for incongruent features compared to congruent ones, relative to younger adults. The interaction between Congruence and Similarity (B = −0.07, t (245) = −5.31, p < 0.001) shows that high similarity decreases RT for congruent features but increases RT for incongruent features. The main effect of Age and the interaction between Similarity and Age were non-significant. The key behavioral finding is a significant three-way interaction between Age Group, Similarity, and Congruence on RT for semantic feature judgments (B = −0.09, t (249) = −3.77, p < 0.001). This three-way interaction indicates that the influence of similarity on reaction time varies by age group and congruence condition. Specifically, high similarity facilitates faster responses in congruent conditions but hinders responses in incongruent conditions, with older adults showing a greater delay in rejecting incongruent features with high similarity. The covariate of education was not significant (B = −0.01, t (245) = −0.56, p = 0.57), indicating that differences in reaction times between younger and older adults were not accounted for by variations in their years of education.

In addition to the primary GLMM analysis, we further investigated the relationship between cosine similarity as a continuous variable and RT by fitting separate linear models for each combination of age group and congruity condition (see Supplementary Fig. 1). The slopes of these relationships were examined to determine if they were statistically significant. For both younger and older adults, cosine similarity was significantly negatively correlated with RT in congruent conditions (Younger: B = −0.179, p < 0.001; Older: B = −0.155, p < 0.001), indicating that higher similarity facilitated faster retrieval. Conversely, cosine similarity was significantly positively correlated with RT in incongruent conditions (Younger: B = 0.201, p < 0.001; Older: B = 0.324, p < 0.001), suggesting that higher similarity increased retrieval

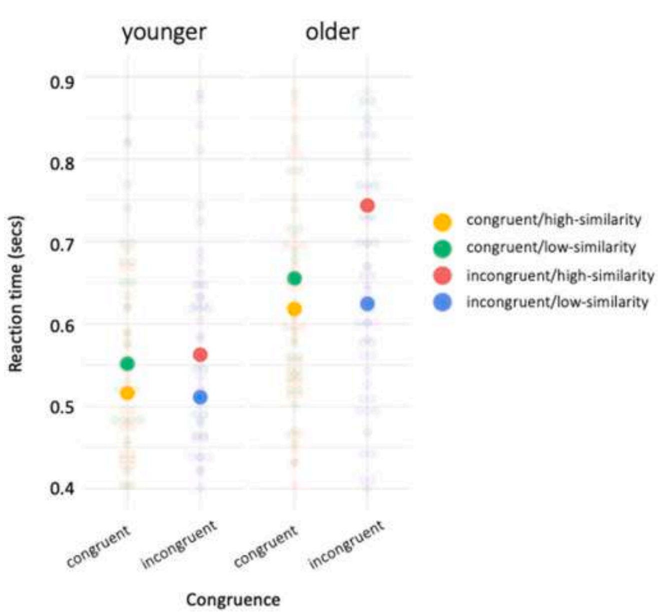

Fig. 3. Behavioral results, reaction time as a function of condition. Younger adults (left) and older adults (right) show an interaction between similarity and condition. Highly similar target-feature pairs facilitate retrieval from semantic memory when features are congruent with target, but hinders retrieval when they are incongruent. Highly similar but incongruent condition shows significant age-related reaction time increase.

difficulty. To statistically compare the slopes between younger and older adults for both congruent and incongruent conditions, we fit linear models including an interaction term between cosine similarity and age group. For the congruent condition, the interaction term between cosine similarity and age group was not significant (B = 0.0237, p = 0.584), suggesting that the effect of cosine similarity on reaction time did not significantly differ between younger and older adults. However, for the incongruent condition, the interaction term was significant (B = 0.123, p = 0.0128), indicating that the effect of cosine similarity on reaction time differed between younger and older adults. These findings suggest that while the effect of semantic similarity on retrieval speed remains comparable between age groups in congruent conditions, in incongruent conditions, older adults show a greater delay with higher similarity.

3.2. EEG

We first ran an omnibus 2 Age Group (young, old) x 4 condition (congruent/high-similarity, congruent/low-similarity, incongruent/high-similarity, incongruent/low-similarity) factorial ANOVA to identify spatial locations and time windows showing significant differences between conditions for more targeted analyses of the N400 and.

LFE. Raster plots showing significant effects can be seen in Fig. 4 along with representative ERPs for each group. We found a significant Age x Condition cluster (p = 0.0001) that spanned from 360 to 1480ms, and included 20 electrodes: C3, C4, CP1, CP2, CP5, CP6, F3, F4, F7, F8, FC1, FC2, FC5, FC6, FT10, FT9, Fz, P3, P4, and P8. The cluster had a temporal peak at 832ms and a spatial peak at electrode F3. We next used this subset of electrodes and time window for all further analysis in order to remove channels and time windows of no interest (i.e. insensitive to our task conditions). We conducted analyses comparing similarity conditions in subsequent analyses separately for congruent and incongruent conditions, focusing on specific regions and time windows of interest for the two ERPs of interest (N400 and LFE). We split analyses by congruency conditions because our hypotheses for these effects were related to semantic similarity and to reduce the influence of the response confound inherent in congruency comparisons (i.e. Yes and No responses for congruent and incongruent conditions, respectively).

For the N400 component, we predicted an age-related attenuation of the high vs. low target-feature similarity modulation, particularly for the congruent condition, because in a denser semantic space, as in aging, high and low similarity features should be more related and less unexpected. We ran a two factorial ANOVA cluster analysis, one for the congruent trials and the other for the incongruent trials: Age Group (young, old) x 2 Similarity (high, low). We included the 20 condition-significant electrodes and timepoints between 350 and 550ms, in which the N400 component is observed. Raster plots and ERPs are shown in Fig. 5. For the congruent target-features pairs, we found a significant Age × Similarity interaction (p = 0.008) in a cluster of electrodes with a spatial peak at electrode F3 and a temporal peak at 554ms. For the incongruent target-features pairs, we found a fronto-central cluster of electrodes in which there was an Age × Similarity interaction (p = 0.02) with a spatial peak at C3 and a temporal peak at 554ms. As can be seen in Fig. 5, the N400 similarity modulation, indicating greater negativity in response to low similarity features compared to high similarity features, was larger for younger than older adults. To test whether the age-related attenuation differed between congruent and incongruent conditions, we ran a 2 Age (young, old) x 2 Congruence (congruent, incongruent) x 2 Channel (F3, C3) ANOVA on the similarity difference scores (high-low). We selected F3 and C3 because they were the spatial peak of the congruent and incongruent clusters, respectively. There was a main effect of Age (F (1,392) = 910.08, p < 0.001; η_p^2 = 0.70) and Congruence (F (1,392) = 90.27, p < 0.001; η_p^2 = 0.19). The interaction between Channel and Age was significant (F (1,392) = 13.26, p < 0.001; η_p^2 = 0.03), as was the three-way interaction between Channel, Age and Congruence (F (1, 392) = 5.32, p = 0.022; η_p^2 = 0.01). Critically, we found that the interaction between Congruence and Age

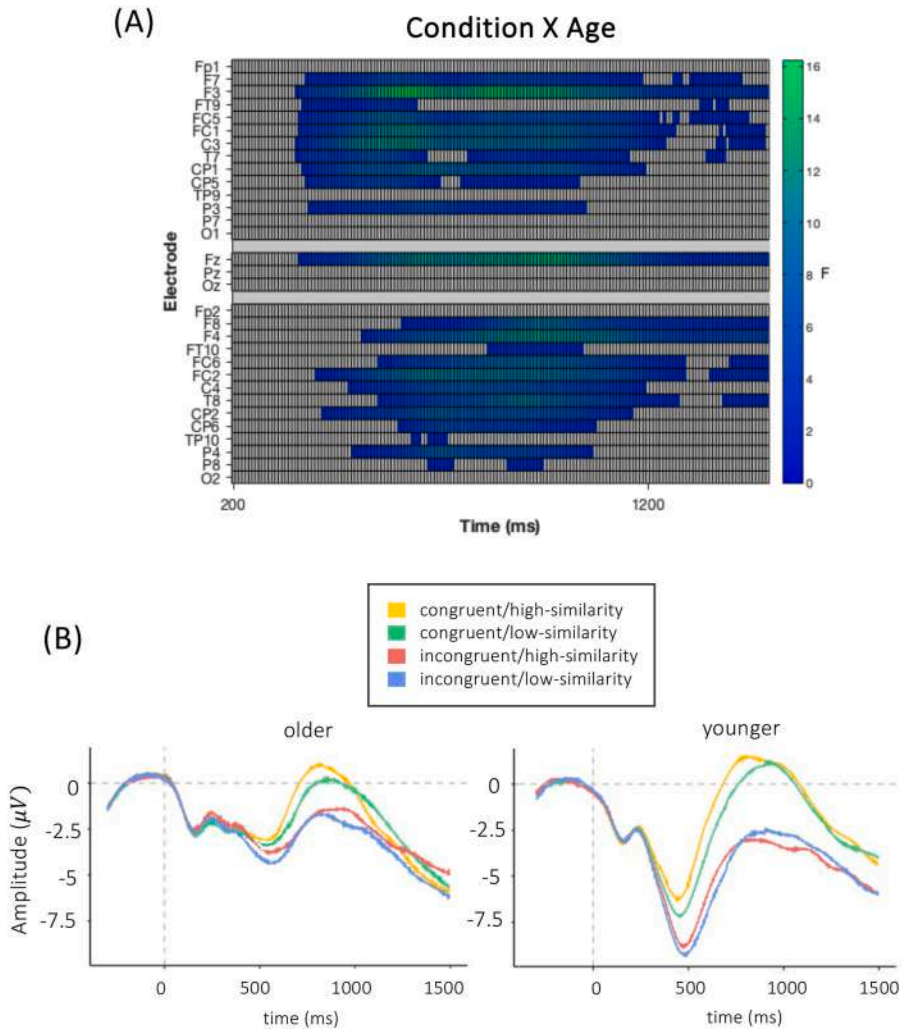

Fig. 4. Omnibus mass univariate and spatial peak F3 ERPs for all conditions. (A) Results from mass univariate cluster analysis show bilateral clusters for a 2 (age: young, old) x 4 (condition: congruent/high-similarity, congruent/low-similarity, incongruent/high-similarity, incongruent/low-similarity) factorial ANOVA. (B) ERPs for electrode F3, the spatial peak of age × condition interaction.

was statistically significant (F (1, 392) = 152.95, $p < 0.001$; $\eta_p^2 = 0.28$). Follow-up analyses revealed significant N400 differences between high and low similarity features for both younger and older adults during congruent trials. High similarity pairs elicited a less negative N400 amplitude for younger adults (t (198) = 4.14, $p < 0.001$), and for older adults (t (193) = 3.32, $p < 0.001$). In contrast, during incongruent trials, a significant difference in N400 amplitudes between high and low similarity pairs was observed for younger adults (t (198) = 2.35, p = 0.02), but not for older adults (t (193) = 1.92, p = 0.057). These results indicate that the influence of congruence on the difference in N400 amplitude between high and low similarity pairs varies by age. Specifically, the neural signature of younger adults shows a significant N400 difference between high and low similarity features across both congruent and incongruent conditions, with high similarity pairs eliciting a smaller (less negative) N400 amplitude than low similarity pairs. In contrast, older adults exhibit a reduced N400 effect in incongruent conditions, suggesting an age-related attenuation in neural responsiveness to semantic similarity when the pairs are incongruent. Conversely, in congruent conditions, the N400 amplitude in older adults shows a more pronounced distinction between high and low similarity pairs, with high similarity pairs eliciting a smaller N400 effect, similar to the pattern observed in younger adults.

Based on our second hypothesis for the LFE, that to-be-rejected (i.e. incongruent) features high in semantic similarity should engage monitoring processes more than those low in similarity especially for older adults, we ran another set of factorial ANOVA cluster analyses separately for the congruent and incongruent trials: Age Group (young, old) x 2 similarity (high, low) (see Fig. 6 for raster plots and ERPs). As for the N400 analyses, we included the 20 condition-significant electrodes from the omnibus mass univariate ANOVA, but for the LFE component, we selected a later time range (800–1500ms), consistent with the literature (Brouwer and Crocker, 2017). There was a significant Age x Similarity effect (p = 0.0001) for congruent trials centered around electrode F8 and with a temporal peak of 1088ms. For incongruent trials, we also found a significant Age × Similarity interaction (p = 0.007), and the peak electrode with the most sustained interaction was F4. To compare the LFE effect across congruent and incongruent conditions, we ran a 2 Age (young, old) x 2 Congruence (congruent, incongruent) x 2 Channel (F8, F4) ANOVA on the similarity difference scores (high-low). We selected F8 and F4 because they were the peaks of significant sustained clusters in the congruent and incongruent trials. We found a main effect of Age (F (1,1384) = 22.61, $p < 0.001$; η_p^2 = 0.02), Congruence (F (1,1384) = 56.39, $p < 0.001$; η_p^2 = 0.04), and Channel (F (1,1384) = 81.16, $p < 0.001$; η_p^2 = 0.06). There was no interaction between Condition and Channel, or Condition, Age and Channel. The interaction between Congruence and Age was statistically significant (F (1, 1384) = 1060.88, $p < 0.001$; η_p^2 = 0.43). During incongruent trials, older adults exhibited a significant LFE difference (t

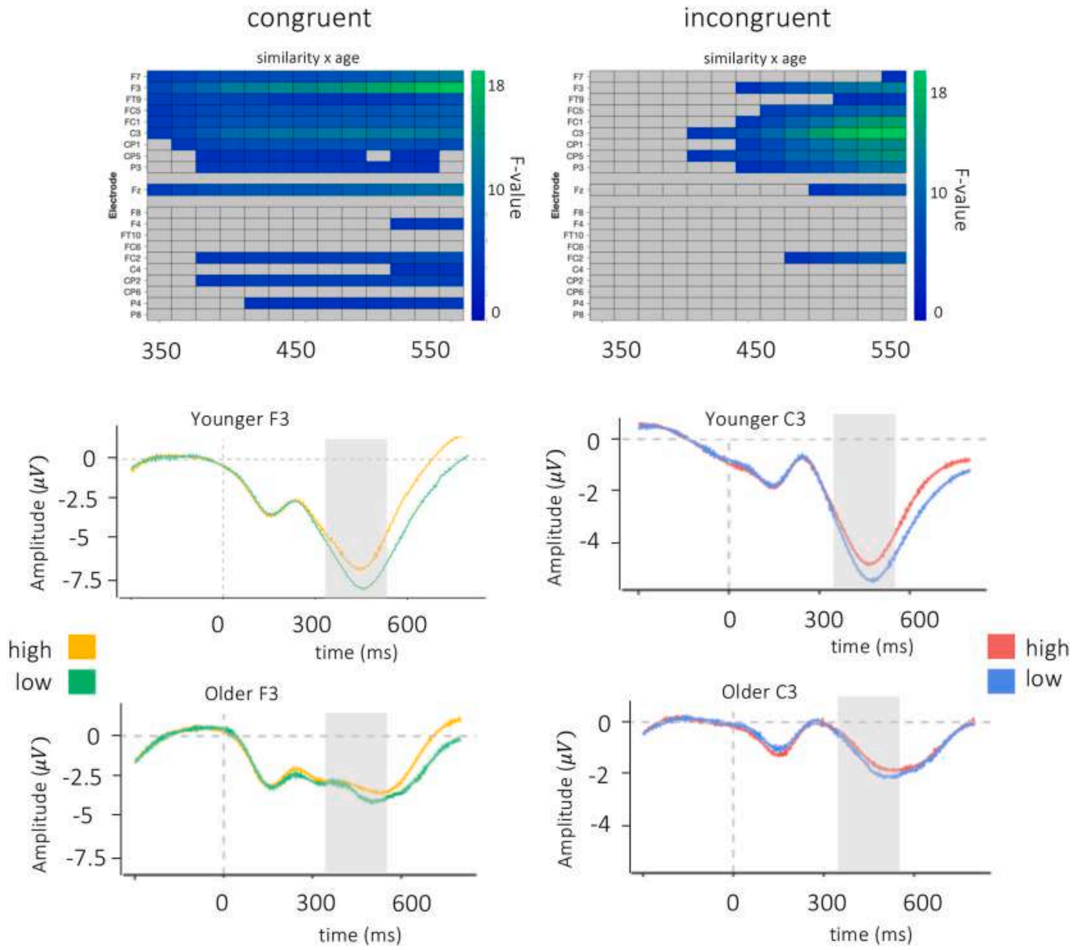

Fig. 5. Age attenuated N400 similarity effect for congruent (left column), but not incongruent (right column) target-feature pairs. (A) Mass univariate cluster analyses show significant age × similarity interaction in left frontal regions. (B) Group-averaged ERPs from electrodes F3 and C3 where the congruent and incongruent spatial peaks were observed. Highlighted area shows 350–550ms.

(680) = 5.31, $p < 0.001$), while no significant difference was observed for younger adults (t (697) = −1.01, p = 0.311). This indicates that the LFE is influenced by both the age of the participants and the congruence of the stimuli. For older adults, the LFE (sustained difference between high and low similarity) was larger during incongruent trials. In contrast, younger adults exhibited a more pronounced LFE during congruent trials, revealing an opposite pattern between the age groups.

4. Discussion

The accumulation of knowledge over a lifetime shapes how we store and access information, making it more complex and interconnected. This study illustrates how the increasing richness of semantic memory with age affects the way we retrieve and distinguish between concepts, especially when they are closely related. The denser organization of knowledge that comes with experience influences both the speed and nature of our cognitive processes. A distributional model of semantic memory allowed us to capture age differences in both behavioral and neural dynamics of semantic cognition in a semantic feature verification task. Our key behavioral finding is that older adults, more than young adults, take significantly longer to correctly reject a semantic feature as being incongruent when it is high vs. low in semantic similarity to the target. ERP results reveal that older adults have an attenuated neural response to semantically congruent features of a target word (N400) and show an extended search (LFE) that differentiates trials based on their distance in vector space i.e. semantic similarity.

As predicted, in both younger and older adults we found that semantic similarity between a target-feature pair facilitates semantic retrieval when it is a congruent feature but hurts it when it is an incongruent feature. This is especially true for older adults, who show a significant increase in response time for rejection of incongruent/high-similarity features. How might these behavioral findings relate to theories of semantic memory organization? Collins and Quillian (1969) proposed the unsuccessful search hypothesis for false responses in sentence verification tasks. Inspired by Sternberg's (1966) (Sternberg, 1966) "self-terminating search" it suggests that false responses are the result of failed search in favor of a true response (Ergen et al., 2012). An extension of that theory, the search and destroy hypothesis, proposes that the connections between nodes are progressively checked before rejection. In this way, reaction times would increase when two concepts have more shared connections, or associated features. Our reaction time results contradict the unsuccessful search hypothesis because we did not observe longer verification times for false features independent of semantic similarity. But the search and destroy hypothesis is conceptually similar to our semantic space theory – we think that increased similarity, based on overlapping and shared features, results in a longer reaction time, especially when those overlapping features need to be rejected (i.e. incongruent trials). This is in line with the feature comparison model (Smith et al., 1974), in which reaction time for false statements is predicted to increase as the overall similarity between two items increases. This slowing effect was more pronounced in older adults, consistent with the idea that as we accumulate knowledge, there are more features to compare. One alternative possibility is that older adults take longer to make a response because the concepts are not available to them, as has

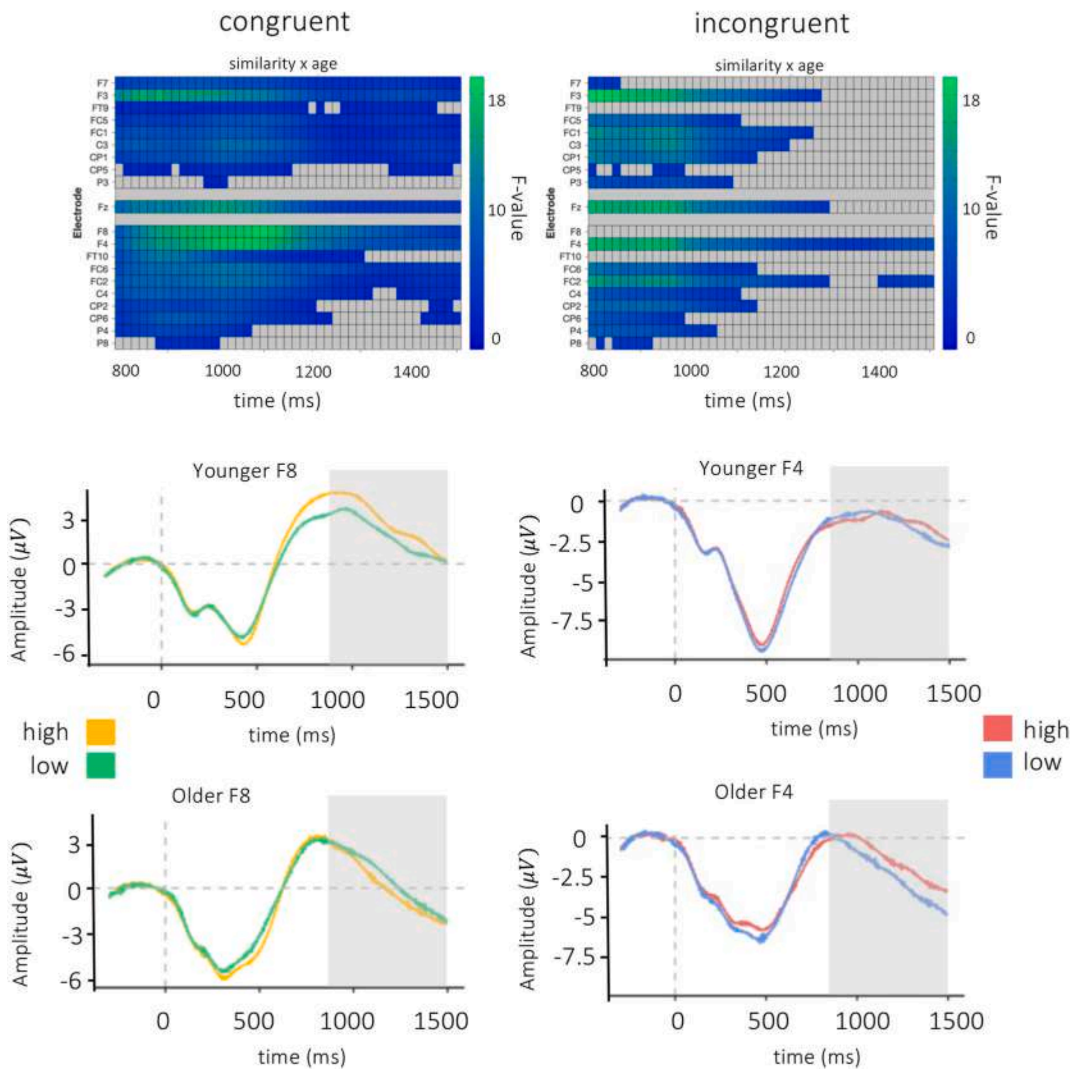

Fig. 6. LFE reflects sustained similarity-related activation in older adults. (B) Mass univariate cluster analyses show significant age × similarity interaction peaking at electrode F8 for congruent, and sustained activation in F4 for incongruent. (B) Group-averaged ERPs from electrodes F8 and F4 where similarity-related age effects were observed. Highlighted area shows neural dynamics of extended search from 800 to 1500 ms.

been proposed in the working memory literature (Basak and Verhaeghen, 2011). However, we found that older people were even more familiar with the word stimuli than were younger people. We take this as further evidence that older adults were searching through a densely populated semantic space - where increased relatedness between features selectively hinders performance for incongruent but high-similarity pairs.

For our N400 component of interest, we found an age-related attenuation of the similarity effect for congruent, compared to incongruent, target-feature pairs. Specifically, in younger adults to a greater extent than older adults, N400 magnitude was greater for low than high similarity target-feature pairs. This finding is consistent with a theory in which older adults' denser semantic space increases the shared feature overlap between concepts. Therefore, the N400 could be invertedly indexing the number of representations that are activated during semantic search. In the younger adults, high-similarity features activate many nearby features, whereas low-similarity features activate fewer. However, for the older adults with a densely populated semantic space, both high and low target-feature pairs may activate many nearby features. It could be that feature activation in a semantic space acts much like semantic priming, where nearby features are activated proportional to their shared feature overlap. Semantic priming occurs when the processing of a word is influenced by the prior exposure to a related stimulus (Meisner, 2012). The N400 is attenuated with repeated priming of related word pairs (Taylor and Burke, 2002), and older adults demonstrate greater semantic priming than younger adults (Kiang et al., 2013). Extending this idea, the attenuated N400 in older adults for congruent trials could represent the density of their feature space, where both high and low similarity features are primed in response to the target word.

Later in semantic retrieval, our study sheds light on the temporal dynamics of search, revealing a distinctive pattern in older adults characterized by a sustained search. This aligns with the notion that the accumulation of knowledge over time significantly influences the trajectory of semantic retrieval. For our LFE component, starting at 800ms and extending until participants make a congruence decision, we find an age-related similarity difference that is the opposite pattern in young and old. We expected both age groups to have a greater LFE for high similarity vs low similarity in both conditions because later frontal activation is thought to index successful recollection (Mecklinger et al., 2007). As expected, we found that older adults show a greater LFE, for incongruent trials, indexing an extended search through semantic space. Our finding that younger adults show an LFE for congruent trials was unexpected. A speculative explanation is that in congruent trials there is less conflict because they don't have to reject competitors. Therefore, the LFE could indicate an age-related difference in competition resolution that is based on congruence and semantic similarity of target-feature pairs (Rose et al., 2019). We suggest that for older adults in particular, the LFE serves as an indicator of post-retrieval monitoring processes. Drawing parallels with findings by Hayama et al. (2008) in the context of episodic memory tasks, where frontal activity at 800ms was associated with evaluation and monitoring dependent on semantic information during retrieval, our study extends this understanding to the semantic feature domain. The LFE and sustained neural activity observed in older adults during semantic retrieval may signify an additional layer of evaluation required to navigate the densely populated semantic space and search for concepts in close proximity.

The Inhibitory Deficit Hypothesis provides a framework for understanding the potential mechanisms underlying semantic cognition in older adults. According to this hypothesis, aging is associated with a decline in the ability to inhibit irrelevant information in various cognitive domains, including memory retrieval (Hasher et al., 2007; Hasher and Zacks, 1988). In the current study, the inhibitory demand is greatest when participants must suppress highly related, but false/-incongruent features (i.e. pencil-has keys), the condition in which older adults were slowest. In a denser semantic space, such as that occurs in aging, there are more highly related features to inhibit. We propose that a denser semantic space is parsimonious with a theory of inhibition, where features are accumulated over experience and therefore add more competitors to the search process. The sustained LFE for older individuals, reflecting a search process with more features to select from, is also consistent with the inhibition deficit hypothesis. That is, when semantic space is denser, inhibition demands are higher and older adults are slower to suppress the semantically related features. However, our supplementary analyses reveal that the impact of semantic similarity on reaction time was only significant in incongruent conditions, not congruent ones. This suggests that the inhibitory demands are indeed greater for older adults when dealing with semantically related but incorrect features. If inhibition were the primary factor, we might expect this effect across both congruent and incongruent conditions. However, our results indicate that this delay in older adults is specific to incongruent conditions, reinforcing the idea that accumulating semantic knowledge influences cognitive processes in aging by increasing the difficulty of suppressing incorrect but related features.

Potential limitations of our approach are the sole use of aging as an approximate model for semantic knowledge accumulation. Individual differences such as cultural influences (Goyal et al., 2020; Machery et al., 2004), exercise habits (Day and Loprinzi, 2019; Loprinzi and Edwards, 2018; Won et al., 2019), and genetic predispositions (Gong et al., 2012) have been found to affect semantic memory. Additionally, our reliance on a sample representing only two age groups constrains our ability to draw nuanced individual-level conclusions. A suggested avenue for future research involves adopting a lifespan approach, capturing participants across a broader age spectrum. This approach would enable us to explore the hypothesis that multiple episodic exposures to a concept or item contribute to the observed increase in semantic space density over time. While our study serves as a valuable proxy for understanding how increased semantic density might influence cognitive processes, future research could enhance these insights by directly comparing vector space models of semantic representations in older versus younger adults. For instance, comparing pairwise concept ratings projected into a high-dimensional space could offer a more precise and nuanced understanding of how age-related changes in semantic memory organization impact retrieval dynamics.

In conclusion, our study addresses the conceptual landscape of semantic memory, specifically exploring the impact of aging on the density of semantic space. We provide evidence that a greater accumulation of knowledge as we age influences semantic retrieval because the representational space itself is denser with more features.

CRediT authorship contribution statement

Rebecca A. Cutler: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Soroush Mirjalili:** Writing – review & editing, Software, Investigation. **Priscilla Pham:** Writing – review & editing, Investigation. **Hita Devulapalli:** Writing – review & editing, Investigation. **Sabuhee Zafar:** Writing – review & editing, Investigation. **Audrey Duarte:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization.

Declarations of competing interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2025.109083.

Data availability

Data will be made available on request.

References

Alejandro, R.J., Packard, P.A., Steiger, T.K., Fuentemilla, L., Bunzeck, N., 2021. Semantic congruence drives long-term memory and similarly affects neural retrieval dynamics in young and older adults. Front. Aging Neurosci. 13, 683908.

Basak, C., Verhaeghen, P., 2011. Aging and switching the focus of attention in working memory: age differences in item availability but not in item accessibility. J. Gerontol. B Psychol. Sci. Soc. Sci. 66 (5), 519–526.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Software 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Brouwer, H., Crocker, M.W., 2017. On the proper treatment of the N400 and P600 in language comprehension. Front. Psychol. 8, 1327.

Chiou, R., Humphreys, G.F., Jung, J., Ralph, M.A.L., 2018. Controlled semantic cognition relies upon dynamic and flexible interactions between the executive 'semantic control'and hub-and-spoke 'semantic representation'systems. Cortex 103, 100–116.

Collins, A.M., Quillian, M.R., 1969. Retrieval time from semantic memory. J. Verb. Learn. Verb. Behav. 8 (2), 240–247.

Collins, A.M., Quillian, M.R., 1970. Facilitating retrieval from semantic memory: the effect of repeating part of an inference. Acta Psychol. 33, 304–314.

Crum, R.M., Anthony, J.C., Bassett, S.S., Folstein, M.F., 1993. Population-based norms for the Mini-Mental State Examination by age and educational level. JAMA 269 (18), 2386–2391.

Cruse, D., Wilding, E.L., 2009. Prefrontal cortex contributions to episodic retrieval monitoring and evaluation. Neuropsychologia 47 (13), 2779–2789. https://doi.org/10.1016/j.neuropsychologia.2009.06.003.

Curran, T., Schacter, D.L., Johnson, M.K., Spinks, R., 2001. Brain potentials reflect behavioral differences in true and false recognition. J. Cognit. Neurosci. 13 (2), 201–216. https://doi.org/10.1162/089892901564261.

Davis, C.P., Yee, E., 2021. Building semantic memory from embodied and distributional language experience. WIREs Cognitive Science 12 (5), e1555. https://doi.org/10.1002/wcs.1555.

Day, S., Loprinzi, P., 2019. Effect of acute moderate-intensity exercise on autobiographical episodic memory and semantic memory. OBM Integrative and Complementary Medicine 4 (3), 1–18.

Deerwester, S., Dumais, S.T., Furnas, G.W., Landauer, T.K., Harshman, R., 1990. Indexing by latent semantic analysis. J. Am. Soc. Inf. Sci. 41 (6), 391–407. https://doi.org/10.1002/(SICI)1097-4571(199009)41:6<391::AID-ASI1>3.0.CO;2-9.

Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J. Neurosci. Methods 134 (1), 9–21.

Donaldson, D.I., Rugg, M.D., 1999. Event-related potential studies of associative recognition and recall: electrophysiological evidence for context dependent retrieval processes. Cognit. Brain Res. 8 (1), 1–16. https://doi.org/10.1016/S0926-6410(98)00051-2.

Ergen, M., Yildirim, E., Uslu, A., Gürvit, H., Demiralp, T., 2012. P3 response during short-term memory retrieval revisited by a spatio-temporal analysis. Int. J. Psychophysiol. 84 (2), 205–210. https://doi.org/10.1016/j.ijpsycho.2012.02.009.

Federmeier, K.D., Kutas, M., 2005. Aging in context: age-related changes in context use during language comprehension. Psychophysiology 42 (2), 133–141. https://doi.org/10.1111/j.1469-8986.2005.00274.x.

Fields, E.C., 2017. Factorial mass univariate ERP toolbox. Github *[Computer software]*. https://scholar.google.com/scholar?cluster=9963970014308988598&hl=en&inst=569367360547434339&oi=scholarr.

Frank, S.L., Willems, R.M., 2017. Word predictability and semantic similarity show distinct patterns of brain activity during language comprehension. Language, Cognition and Neuroscience 32 (9), 1192–1203. https://doi.org/10.1080/23273798.2017.1323109.

Gong, P., Zheng, Z., Chi, W., Lei, X., Wu, X., Chen, D., Zhang, K., Zheng, A., Gao, X., Zhang, F., 2012. An association study of the genetic polymorphisms in 13 neural plasticity-related genes with semantic and episodic memories. J. Mol. Neurosci. 46 (2), 352–361. https://doi.org/10.1007/s12031-011-9592-5.

Goyal, N., Adams, M., Cyr, T.G., Maass, A., Miller, J.G., 2020. Norm-based spontaneous categorization: cultural norms shape meaning and memory. J. Pers. Soc. Psychol. 118 (3), 436–456. https://doi.org/10.1037/pspi0000188.

Griffiths, T.L., Steyvers, M., Tenenbaum, J.B., 2007. Topics in semantic representation. Psychol. Rev. 114 (2), 211.

Groppe, D.M., Urbach, T.P., Kutas, M., 2011a. Mass univariate analysis of event-related brain potentials/fields I: a critical tutorial review. Psychophysiology 48 (12), 1711–1725. https://doi.org/10.1111/j.1469-8986.2011.01273.x.

Groppe, D.M., Urbach, T.P., Kutas, M., 2011b. Mass univariate analysis of event-related brain potentials/fields II: simulation studies. Psychophysiology 48 (12), 1726–1737. https://doi.org/10.1111/j.1469-8986.2011.01272.x.

Groppe, D.M., Urbach, T.P., Kutas, M., 2011c. Mass univariate analysis of event-related brain potentials/fields I: A critical tutorial review. Psychophysiology 48 (12), 1711–1725.

Hasher, L., Lustig, C., Zacks, R.T., 2007. Inhibitory mechanisms and the control of attention. Variation in Working Memory 19, 227–249.

Hasher, L., Zacks, R.T., 1988. Working memory, comprehension, and aging: a review and a new view. Psychol. Learn. Motiv. 22, 193–225.

Hayama, H.R., Johnson, J.D., Rugg, M.D., 2008. The relationship between the right frontal old/new ERP effect and post-retrieval monitoring: specific or non-specific? Neuropsychologia 46 (5), 1211–1223. https://doi.org/10.1016/j.neuropsychologia.2007.11.021.

Horne, E.D., Koen, J.D., Hauck, N., Rugg, M.D., 2020. Age differences in the neural correlates of the specificity of recollection: an event-related potential study. Neuropsychologia 140, 107394. https://doi.org/10.1016/j.neuropsychologia.2020.107394.

Jasper, H.H., 1958. Ten-twenty electrode system of the international federation. Electroencephalogr. Clin. Neurophysiol. 10, 371–375.

Jones, M.N., 2019. When does abstraction occur in semantic memory: insights from distributional models. Language, Cognition and Neuroscience 34 (10), 1338–1346. https://doi.org/10.1080/23273798.2018.1431679.

Kiang, M., Patriciu, I., Roy, C., Christensen, B.K., Zipursky, R.B., 2013. Test–retest reliability and stability of N400 effects in a word-pair semantic priming paradigm. Clin. Neurophysiol. 124 (4), 667–674. https://doi.org/10.1016/j.clinph.2012.09.029.

Kounios, J., Holcomb, P.J., 1992. Structure and process in semantic memory: evidence from event-related brain potentials and reaction times. J. Exp. Psychol. Gen. 121 (4), 459.

Kutas, M., Federmeier, K.D., 2011. Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). Annu. Rev. Psychol. 62 (1), 621–647. https://doi.org/10.1146/annurev.psych.093008.131123.

Kwantes, P.J., 2005. Using context to build semantics. Psychonomic Bull. Rev. 12 (4), 703–710.

Landauer, T.K., Dumais, S.T., 1997. A solution to Plato's problem: the latent semantic analysis theory of acquisition, induction, and representation of knowledge. Psychol. Rev. 104 (2), 211.

Lindborg, A., Musiolek, L., Ostwald, D., Rabovsky, M., 2023. Semantic surprise predicts the N400 brain potential. Neuroimage: Report 3 (1), 100161. https://doi.org/10.1016/j.ynirp.2023.100161.

Lo, S., Andrews, S., 2015. To transform or not to transform: using generalized linear mixed models to analyse reaction time data. Front. Psychol. 6. https://www.frontiersin.org/articles/10.3389/fpsyg.2015.01171.

Loprinzi, P.D., Edwards, M.K., 2018. Exercise and cognitive-related semantic memory function. J Cognit Behav Psychotherap Res 7 (2), 51–52.

Lund, K., Burgess, C., 1996. Producing high-dimensional semantic spaces from lexical co-occurrence. Behav. Res. Methods Instrum. Comput. 28 (2), 203–208. https://doi.org/10.3758/BF03204766.

Machery, E., Mallon, R., Nichols, S., Stich, S.P., 2004. Semantics, cross-cultural style. Cognition 92 (3), B1–B12.

Malandrakis, N., Potamianos, A., Iosif, E., Narayanan, S., 2013. Distributional semantic models for affective text analysis. IEEE Trans. Audio Speech Lang. Process. 21 (11), 2379–2392. https://doi.org/10.1109/TASL.2013.2277931.

Maris, E., 2012. Statistical testing in electrophysiological studies. Psychophysiology 49 (4), 549–565. https://doi.org/10.1111/j.1469-8986.2011.01320.x.

Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG-and MEG-data. J. Neurosci. Methods 164 (1), 177–190.

McRae, K., Cree, G.S., Seidenberg, M.S., Mcnorgan, C., 2005. Semantic feature production norms for a large set of living and nonliving things. Behav. Res. Methods 37 (4), 547–559. https://doi.org/10.3758/BF03192726.

Mecklinger, A., Johansson, M., Parra, M., Hanslmayr, S., 2007. Source-retrieval requirements influence late ERP and EEG memory effects. Brain research 1172, 110–123.

Meisner, B.A., 2012. A meta-analysis of positive and negative age stereotype priming effects on behavior among older adults. J. Gerontol.: Ser. Bibliogr. 67B (1), 13–17. https://doi.org/10.1093/geronb/gbr062.

Molloy, D.W., Alemayehu, E., Roberts, R., 1991. Reliability of a standardized mini-mental state examination compared with the traditional mini-mental state examination. Am. J. Psychiatr. 148 (1), 102–105.

Packard, P.A., Steiger, T.K., Fuentemilla, L., Bunzeck, N., 2020. Neural oscillations and event-related potentials reveal how semantic congruence drives long-term memory in both young and older humans. Sci. Rep. 10 (1), 9116.

Payne, B.R., Federmeier, K.D., 2018. Contextual constraints on lexico-semantic processing in aging: evidence from single-word event-related brain potentials. Brain Res. 1687, 117–128.

Pennington, J., Socher, R., Manning, C., 2014. Glove: Global Vectors for Word Representation, pp. 1532–1543.

Pereira, F., Lou, B., Pritchett, B., Ritter, S., Gershman, S.J., Kanwisher, N., Botvinick, M., Fedorenko, E., 2018. Toward a universal decoder of linguistic meaning from brain activation. Nat. Commun. 9 (1), 963.

Pion-Tonachini, L., Kreutz-Delgado, K., Makeig, S., 2019. ICLabel: an automated electroencephalographic independent component classifier, dataset, and website. Neuroimage 198, 181–197. https://doi.org/10.1016/j.neuroimage.2019.05.026.

Raaijmakers, J.G., Shiffrin, R.M., 1980. SAM: a theory of probabilistic search of associative memory. Psychol. Learn. Motiv. 14, 207–262.

Rabovsky, M., McRae, K., 2014. Simulating the N400 ERP component as semantic network error: insights from a feature-based connectionist attractor model of word meaning. Cognition 132 (1), 68–89.

Ralph, M.A.L., Jefferies, E., Patterson, K., Rogers, T.T., 2017. The neural and computational bases of semantic cognition. Nat. Rev. Neurosci. 18 (1). https://doi.org/10.1038/nrn.2016.150. Article 1.

Rosch, E., 1975. Cognitive representations of semantic categories. J. Exp. Psychol. Gen. 104 (3), 192.

Rose, S.B., Aristei, S., Melinger, A., Abdel Rahman, R., 2019. The closer they are, the more they interfere: semantic similarity of word distractors increases competition in language production. J. Exp. Psychol. Learn. Mem. Cognit. 45 (4), 753–763. https://doi.org/10.1037/xlm0000592.

Rugg, M.D., Curran, T., 2007. Event-related potentials and recognition memory. Trends Cognit. Sci. 11 (6), 251–257.

Sahlgren, M., Lenci, A., 2016. The Effects of Data Size and Frequency Range on Distributional Semantic Models (arXiv:1609.08293). arXiv. http://arxiv.org/abs/1609.08293.

Sajin, S.M., Connine, C.M., 2014. Semantic richness: the role of semantic features in processing spoken words. J. Mem. Lang. 70, 13–35. https://doi.org/10.1016/j.jml.2013.09.006.

Shiffrin, R.M., Steyvers, M., 1997. A model for recognition memory: REM—retrieving effectively from memory. Psychonomic Bull. Rev. 4 (2), 145–166. https://doi.org/10.3758/BF03209391.

Smith, E.E., Shoben, E.J., Rips, L.J., 1974. Structure and process in semantic memory: a featural model for semantic decisions. Psychol. Rev. 81 (3), 214.

Sternberg, S., 1966. High-speed scanning in human memory. Science 153 (3736), 652–654. https://doi.org/10.1126/science.153.3736.652.

Steyvers, M., Shiffrin, R.M., Nelson, D.L., 2004. Word association spaces for predicting semantic similarity effects in episodic memory. Experimental Cognitive Psychology and its Applications: Festschrift in Honor of Lyle Bourne, Walter Kintsch. Thomas Landauer, pp. 237–249.

Taylor, J.K., Burke, D.M., 2002. Asymmetric aging effects on semantic and phonological processes: naming in the picture-word interference task. Psychol. Aging 17 (4), 662.

Thomson, D.M., Tulving, E., 1970. Associative encoding and retrieval: weak and strong cues. J. Exp. Psychol. 86 (2), 255–262.

Tiedt, H.O., Ehlen, F., Klostermann, F., 2020. Age-related dissociation of N400 effect and lexical priming. Sci. Rep. 10 (1), 20291.

van Ede, F., Maris, E., 2016. Physiological plausibility can increase reproducibility in cognitive neuroscience. Trends Cognit. Sci. 20 (8), 567–569.

Wlotko, E.W., Federmeier, K.D., 2012. Age-related changes in the impact of contextual strength on multiple aspects of sentence comprehension. Psychophysiology 49 (6), 770–785. https://doi.org/10.1111/j.1469-8986.2012.01366.x.

Wlotko, E.W., Federmeier, K.D., Kutas, M., 2012. To predict or not to predict: age-related differences in the use of sentential context. Psychol. Aging 27 (4), 975.

Won, J., Alfini, A.J., Weiss, L.R., Michelson, C.S., Callow, D.D., Ranadive, S.M., Gentili, R.J., Smith, J.C., 2019. Semantic memory activation after acute exercise in healthy older adults. J. Int. Neuropsychol. Soc. 25 (6), 557–568.

Zhuang, J., Johnson, M.A., Madden, D.J., Burke, D.M., Diaz, M.T., 2016. Age-related differences in resolving semantic and phonological competition during receptive language tasks. Neuropsychologia 93, 189–199. https://doi.org/10.1016/j.neuropsychologia.2016.10.016.