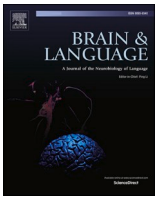
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Spatiotemporal dynamics of abstract and concrete semantic representations

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ABSTRACT

Dual Coding Theories (DCT) suggest that meaning is represented in the brain by a double code: a language-derived code in the Anterior Temporal Lobe (ATL) and a sensory-derived code in perceptual and motor regions. Concrete concepts should activate both codes, while abstract ones rely solely on the linguistic code. To test these hypotheses, the present magnetoencephalography (MEG) experiment had participants judge whether visually presented words relate to the senses while we recorded brain responses to abstract and concrete semantic components obtained from 65 independently rated semantic features. Results evidenced early involvement of anterior-temporal and inferior-frontal brain areas in both abstract and concrete semantic information encoding. At later stages, occipital and occipito-temporal regions showed greater responses to concrete compared to abstract features. The present findings suggest that the concreteness of words is processed first with a transmodal/linguistic code, housed in frontotemporal brain systems, and only after with an imagistic/sensorimotor code in perceptual regions.

1. Introduction

Abstract and concrete semantic representations form fundamental aspects of word meaning. For instance, concrete features (e.g., the color, the sound), as well as abstract features (e.g., clever, wild), contribute to the representation of a fox in semantic knowledge (Binder et al., 2016). Although the ability of the brain to retrieve these representations is at the core of human semantic knowledge, the neural underpinnings of this process are not completely understood. To explain how various sorts of knowledge guide a broad range of behaviors, Dual Coding Theories (DCT; Paivio, 1986, 1991) put forward the idea that, in the brain, semantic knowledge is represented in a dual coding system comprising a linguistic code, and an imagistic/sensorimotor code. In DCT, abstract and concrete concepts can both be represented through the linguistic code, whereas the imagistic/sensorimotor code is available only for concrete aspects of meaning. For instance, our representation of "snow" relies on both our ability to receive and transfer information related to snow and our direct sensorial experience with snow. Concepts like "freedom" and "truth", instead, do not have stable sensorimotor basis and rely mostly on a language-based representation. In experimental psychology, the fact that concrete words are recognized faster (Kroll & Merves, 1986; Schwanenflugel, Kippharnishfeger, Stowe, & Hall, 1988; Schwanenflugel & Stowe, 1989) and memorized better (Allen & Hulme, 2006; de Groot, 1989; Fliessbach, Weis, Klaver, Elger, & Weber, 2006) than abstract words (i.e., the concreteness effect) has been traditionally taken as evidence in favor of the dual coding approach: only concrete concepts can activate both codes (linguistic and sensorimotor), a condition which gives them a processing advantage (Connell & Lynott, 2012; Paivio, 1986). However, the evidence of the concreteness effect in congenitally blind people has cast doubts on this interpretation (Bottini, Morucci, D'Urso, Collignon, & Crepaldi, 2021). Despite lacking a sensory code for visual features, early blind people processed visual unimodal-concrete words (e.g., "red," "multicolor," "transparent") faster than abstract words, showing a concreteness effect that was indistinguishable from the one of sighted people (Bottini et al., 2021) and suggesting that the concreteness advantage is not driven by the availability of a double code for concrete words.

If, on the one hand, behavioral results with blind people are

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inconsistent with a dual code interpretation of the concreteness effect, a recent line of studies exploring the brain basis of visual knowledge in the absence of vision has provided novel neurocognitive evidence for a dual code of semantic knowledge in the brain (see Bi, 2021). Two studies focusing on color representations in sighted and congenitally blind have shown that posterior brain areas in the V4 complex encode the similarity of color words, but only in sighted people (Bottini et al., 2020; Wang, Men, Gao, Caramazza, & Bi, 2020). However, color similarity is also encoded in the dorsal anterior temporal lobe (ATL) in both sighted and blind (Wang et al., 2020). Thus, the dorsal ATL seems to provide a non-sensory code to represent knowledge, both concrete and abstract, whereas a perceptual code for concrete representations relies on posterior perceptual regions and may not be available in the case of sensory deprivation (Bi, 2021).

Beyond research with populations devoid of specific aspects of perceptual experience, functional resonance imaging (fMRI) studies investigating topological as well as functional properties of the semantic network provide additional evidence in favor of a dual-code account of semantic knowledge in the brain (e.g., Bi, 2021; Xu, He, & Bi, 2017). From a network perspective, the dorsal anterior temporal lobe (dATL) and posterior sensory and motor regions are components of dissociable brain systems. The dATL belongs to the high-level linguistic system in the left perisylvian network, encompassing the inferior frontal gyrus, the lateral temporal cortex, and the inferior parietal cortex (for instance, Fedorenko, Behr, & Kanwisher, 2011; Friederici, 2011). It has stronger connections to the other regions in the language network than the sensorimotor regions (Jackson, Hoffman, Pobric, & Lambon Ralph, 2016; Wang et al., 2020). The left perisylvian language network is consistently activated in semantic tasks (Binder, Desai, Graves, & Conant, 2009; Xu et al., 2017), and is considered to play a role in language-supported semantic processing (Xu et al., 2017). Beyond DCTs, other models suggest that both codes are present in the ATL, arranged in a continuous transmodal gradient (e.g., Lambon-Ralph, Jefferies, Patterson, & Rogers, 2017). That is, the ATL is considered a transmodal (i.e., important for all domains and modalities) hub with a linguistic neural code in its dorsal part, and a perceptual code in its ventral part (Hoffman, Binney, & Lambon Ralph, 2015; Visser & Lambon Ralph, 2011).

In contrast, visual regions (including the color region V4 in fusiform and lingual gyri) belong to the highly distributed sensorimotor brain system, (see Wang et al., 2020) which reflects relevant perceptual dimensions of the input such as visual, tactile, auditory, etc. (Barsalou, Simmons, Barbey, & Wilson, 2003; Binder et al., 2005, 2009; Binder & Desai, 2011; Carota, Kriegeskorte, Nili, & Pulvermuller, 2017; Carota, Nili, Pulvermuller, & Kriegeskorte, 2021; Fernandino et al., 2016; Fernandino, Tong, Conant, Humphries, & Binder, 2022; Hauk, Shtyrov, & Pulvermüller, 2008; Hoffman et al., 2015; Kana, Blum, Ladden, & ver Hoef, 2012; Sabsevitz, Medler, Seidenberg, & Binder, 2005). These regions are usually more active for concrete compared to abstract concepts (Binder et al., 2005, 2009; Binder & Desai, 2011; Wang, Conder, Blitzer, & Shinkareva, 2010) and may host sensorimotor simulations of perceptual referents during semantic processing (Carota, Moseley, & Pulvermüller, 2012; Fernandino et al., 2015). However, as fMRI suffers from poor temporal resolution, several questions about the spatiotemporal dynamics of the dual code of knowledge in the brain remain unanswered. For instance, it is unclear whether transmodal/language-derived representations in the ATL are activated before, after, or at the same time as sensorimotor representations in perceptual regions. This missing information is crucial to understand the neural dynamics of conceptual processing and, in particular, how concreteness (abstractness) is encoded in the brain.

To answer this question, we took advantage of the high temporal resolution of magnetoencephalography (MEG) signals combined with source-reconstruction techniques to assess the spatiotemporal dynamics of abstract and concrete semantic representations. Forty-six participants performed a semantic categorization task on 438 written words. Each word referred to a concept (e.g., chair, dog, policeman) that was independently rated across 65 feature dimensions (e.g., color, shape, happiness, arousal, cognition, etc.; Binder et al., 2016). Using principal component analysis (PCA), we reduced the dimensionality of this feature space into one abstract and one concrete semantic principal component. We then used a combination of multiple linear regression analysis and source reconstruction methods to assess neural dynamics of abstract and concrete semantic representations while keeping into account other types of psycholinguistic information processed during visual word recognition.

2. Material and methods

2.1. Participants

Forty-six native Italian speakers (29 female, aged 24.8 ± 4.2 years) participated in the study. All participants were right-handed and had no history of neurological or psychiatric disorders. Before testing, participants gave their written informed consent and received monetary reimbursement for their participation. The experiments were conducted in accordance with the Declaration of Helsinki and were approved by the local ethical committee of the University of Trento.

2.2. Experimental design

Our stimulus set was obtained from an existing work by Binder and colleagues (Binder et al., 2016). Out of 535 English words included in Binder et al. (2016) original study, 438 were translated into Italian (352 nouns in the singular form, 54 verbs in the infinitive tense, and 32 adjectives in the singular masculine form). Selected words could be unambiguously translated into Italian and were presented to the participants only once. Participants were instructed to categorize each stimulus as either related to sensory-perception (i.e., they express something that is related to one or more of the senses), or unrelated to sensory perception. Visual stimuli were projected on a translucent whiteboard (1440 × 1080 pixel resolution) using a ProPixx DLP projector (VPixxTechnologies, Canada) at a 120 Hz refresh rate. Stimulus presentation was controlled via Psychtoolbox (Kleiner, Brainard, & Pelli, 2007) running in a MATLAB 2015a environment. At the beginning of each trial, a 1 s blank screen followed by a 0.5 s fixation cross preceded stimulus appearance. Words appeared in a white monospaced bold font on a dark gray background, covering on average 3.2 degrees of visual angle ($SD = 0.8$). Stimuli remained on the screen for 0.3 s, followed by a 1.7 s blank screen. After this delay, a text ("Was it a word related to the senses? YES - NO") prompted participants' responses via button press operated with the dominant hand's index and middle fingers. The response mapping was counterbalanced across participants. The maximum time given to respond was set to 2 s and was followed by an interstimulus interval randomly jittered between 0.3 s and 0.6 s. Participants were familiarized with a short version of the task (30 trials taken from a different stimulus set) on a portable PC outside the MEG chamber. Each testing session lasted approximately 2 h and was divided into twelve seven-minutes runs separated by eleven short breaks and one 30 min break.

2.3. MEG data acquisition and preprocessing

MEG signals were recorded at a sampling rate of 1 kHz using a whole-head 306 sensor (204 planar gradiometers; 102 magnetometers) Vectorview system (Elekta Neuromag, Helsinki, Finland). The MEG signal was online band-pass filtered between 0.1 and 300 Hz. To continuously determine the position of head in relation to the MEG helmet five head-position indicator coils (HPIs) were employed. Prior to recording individual head shapes were digitized using fiducial points (the nasion and the left and right pre-auricular points) and a minimum of 300 other points on the scalp using a Polhemus FASTRAK 3D digitizer (Fastrak Polhemus, Inc., Colchester, VA, USA).

Bad channels identified through visual inspection were replaced by interpolation. A spatio-temporal variant of signal-space separation (SSS) algorithm implemented in the MaxFilter 2.0 software (Elekta Neuromag ®) was used to isolate external sources of noise from the head-generated signals. Finally, data across different runs was aligned to an individual common head position. Data analysis was done using non-commercial software packages such as Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011), Brainstorm (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011) and custom scripts in a MATLAB 2019a environment. Continuous MEG recordings were high-pass filtered using a two-pass Butterworth filter with a cutoff frequency of 0.1 Hz and segmented from −1.5 s before to 2 s after stimulus onset. Time segments contaminated by artifacts were manually rejected (total data loss of $M = 2.4$ %, $SD = 1.8$ %). For the further encoding analysis, segmented data was low-pass filtered with a 40 Hz Butterworth filter and baseline corrected with respect to a −500 to −100 ms pre-stimulus time window.

2.4. Multiple linear regression analysis

Multiple linear regression analysis of MEG signals was computed following the approach of previous M/EEG studies (Chen et al., 2013, 2015; Hauk et al., 2006, 2009; Miozzo, Pulvermüller, & Hauk, 2015). For each time point, channel and subject we calculated event-related regression coefficients (ERRCs) reflecting the contribution of predictors to the data (Bertero, de Mol, & Pike, 1985). For the present study, we focused on four predictors spanning word-form, lexical and semantic aspects of word retrieval (i.e., word length/duration, word frequency and an abstract and a concrete semantic predictor obtained via dimensionality reduction techniques of a 65 features' space, see 2.5.). Before entering the regression model, regressors of interest (i.e., word length, word frequency, abstract semantic component and concrete semantic component) were i) orthogonalized via varimax rotation and ii) converted to normalized z-scores. To make sure that the varimax rotation effectively eliminated any collinearity issue, we computed the condition number for each X (Belsley, 1982); indeed, there was no collinearity to speak of (all test values < 2, while a value between 10 and 30 indicates the presence of multicollinearity).

2.5. Predictor variables

The present study aimed to explore the role of abstract and concrete semantic dimensions in concepts representation. On this account, we derived our stimulus set from a previous work by Binder and colleagues (Binder et al., 2016). In this work, salience ratings for 65 biologically plausible features and 535 English words were collected. That is, for every word in the database more than one thousand participants were asked to rate how each of the features was associated with that aspect of the experience. Take for instance the word "axe" and 3 exemplary features: Shape, Color and Fearful. Participants were asked to rate from 0 to 6 if they would define an axe as having a characteristic or defining shape? Or a characteristic or defining color? Or as something that makes you feel afraid? The ratings weight the contribution of each of these features to the semantic representation of an axe (e.g., shape has a high contribution, color has a low contribution, fearful has a high contribution). Crucially, features spanned both abstract (e.g., arousal, social, sad) and concrete (e.g., shape sound, smell) domains of conceptual knowledge, thus representing an ideal framework to operationalize our assumptions.

2.5.1. Semantic components

As previously stated, our semantic space comprised more than sixty features. Employing a single model to encode the entire space would not be optimal due to the high intercorrelation of the predictors, leading to a multicollinearity problem. To address this issue, dimensionality reduction techniques (Cunningham & Yu, 2014), such as principal component analysis (PCA) can be employed. PCA generates principal components (PCs) that represent the same data in a new coordinate system, with the first PC typically explaining the highest proportion of data variance. Following the concrete versus abstract labeling provided in the original database (Binder et al., 2016), we separated the entire semantic space (65-features) into concrete features (N = 31) including Vision, Somatic, Audition Gustation, Olfaction and Motor domains, and abstract features (N = 31) including Spatial, Temporal, Causal, Social, Emotion, Drive and Attention domains. Three features, namely Complexity, Practice, Caused were excluded from the analysis due to incomplete ratings. The subdivision in abstract and concrete features proposed by Binder and collaborators is not clear-cut, for instance, sensorimotor dimensions may be associated to abstract ones (e.g., the act of running may have a cause and an objective), and vice versa. However, there is evidence that concrete words score higher in the concrete dimensions compared to abstract ones, and the opposite is true for abstract words (Binder et al., 2016; Troche, Crutch, & Reilly, 2014). Moreover, this arrangement reflects the complexity of our experience and the effect of context, for which every object can be characterized both by abstract and concrete dimensions (Barsalou, Dutriaux, & Scheepers, 2018). Our aim in this experiment was to disentangle the contribution of dimensions that reliably reflect the perceptual and sensorimotor structure of the environment (vision, somatic, audition, etc.) and dimensions that reflect structural knowledge that is less attributable to precise sensorimotor sources (spatial, temporal, emotions, etc.), and thus may rely more exclusively on a verbal code. Thus, each word could be considered as a point in a concrete semantic features' space (see Fig. 1A), and in an abstract semantic features' space (see Fig. 1B). We used PCA to reduce the dimensionality of the dataset and adopted the first concrete semantic component (Fig. 1C; 24.7 % of variance explained) and the first abstract semantic component (Fig. 1D; 27.4 % of the variance explained), to represent the same data in a new one-dimensional coordinate system. Importantly, the resulting semantic components are orthogonal to each other and do not simply reflect how concrete and how abstract a word is, but instead represents concrete and abstract aspects of concepts in a new low-dimensional space that encodes the most salient structural features of the high-dimensional space from which it is derived. For instance, in the concrete principal component, "moose" is more similar to "street" than to "hug", whereas the opposite is true in the abstract principal component (Fig. 1, C–D). A possible limitation to this study is that ratings (and the resulting semantic features) were collected in an English-speaking population (i.e., Binder's et al. work) whereas the participants to our study were Italian. It is plausible that some of these semantic dimensions would be rated differently by Italian and English-speaking participants. However, when we compared semantic features obtained from an Italian-speaking population (Repetto, Rodella, Conca, Santi, & Catricala, 2022) with those obtained by Binder et al. (2016), we observed a good level of agreement (SI Appendix, Table S1), which provides solid validation to our approach.

2.5.2. Linguistic features

We additionally obtained psycholinguistic features for each of the selected words. Word Frequency (in Zipf's scale, M = 4, SD = 0.8; van Heuven, Mandera, Keuleers, & Brysbaert, 2014) was calculated as the frequency of occurrence of a given word in a large corpus of text samples (SUBTLEX-IT; Crepaldi, Amenta, Pawel, Keuleers, & Brysbaert, 2015). Word length was encoded as the number of letters of each word ($M = 6.9$, $SD = 1.6$).

2.6. Source reconstruction

Distributed minimum-norm source estimation (Hämäläinen & Ilmoniemi, 1994) was applied following the standard procedure in Brainstorm (Tadel et al., 2011). Anatomical T1-weighted MRI images were acquired during a separate session in a MAGNETOM Prisma 3 T scanner (Siemens, Erlangen, Germany) using a 3D MPRAGE sequence, 1-mm^3 resolution, TR = 2140 ms, TI = 900 ms, TE = 2.9 ms, flip angle 12°.

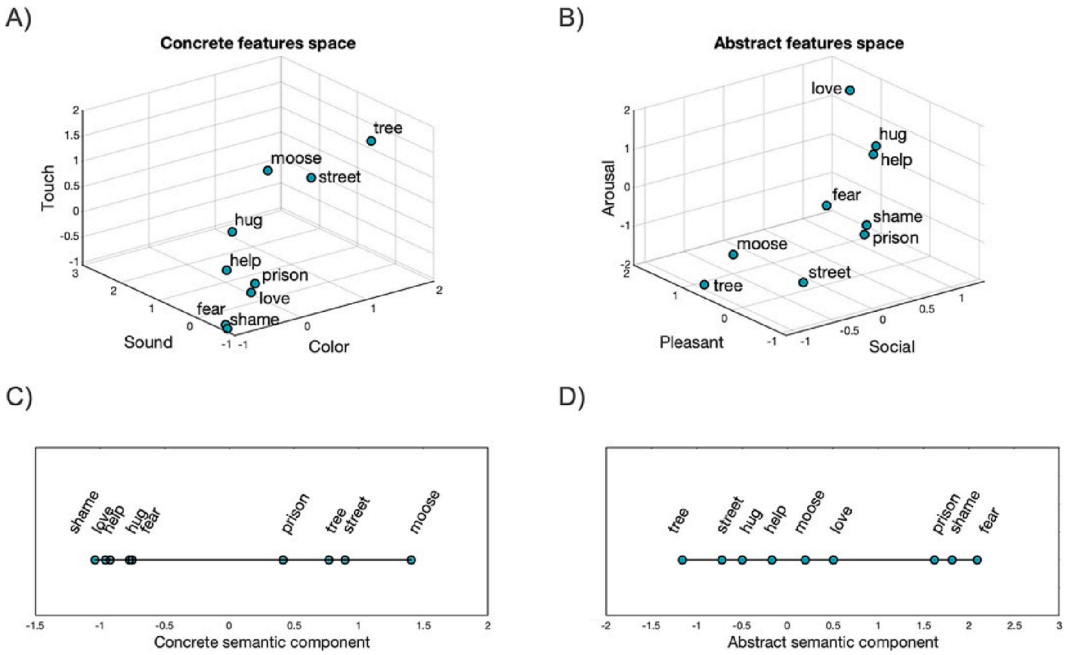


Fig. 1. Dimensionality reduction. A) Schematic representation of a 3-D semantic space where each word is viewed in a coordinate system defined by concrete features such as Touch, Sound and Color (the actual multidimensional space comprised 31 dimensions, here reduced to 3 for visualization purposes). B) Schematic representation of a 3-D semantic space where each word is viewed in a coordinate system defined by abstract features such as Arousal, Pleasant and Social (the actual multidimensional space comprised 31 dimensions). C) Words' weights along the first principal component of the concrete space. D) Words' weights along the first principal component of the abstract space.

Anatomical MRI images were processed using an automated segmentation algorithm of the Freesurfer software (Fischl, 2012). Co-registration of MEG sensor configuration and the reconstructed scalp surfaces was based on ~300 scalp surface locations. When no individual MRI was available (6 participants), we warped participants' head shapes to a standard ICBM152 brain template. The data noise covariance matrix was calculated from the baseline interval (−500 ms to −100 ms) of the different trials. The forward model was obtained using the overlapping spheres method (Huang, Mosher, & Leahy, 1999) as implemented in the Brainstorm software. We then: i) Estimated current density maps for event-related regression coefficients onto a 15,000 vertices boundary element. Dipole sources were assumed to be perpendicular to the cortical surface. ii) Normalized current density values with respect to a −500 ms to −100 ms baseline period (z-transform). iii) Rectified current density values (converted to absolute values). iv) Spatially smoothed the source maps using an 8 mm full width at half the maximum smoothing parameter (FWHM) and, finally, v) the individual results were projected to a default template (ICBM152).

2.7. Sensor-level statistical analysis and visualization

In line with previous studies (Chen et al., 2013, 2015; Hauk et al., 2006, 2009; Miozzo et al., 2015), we depicted the time course of different regressors as the root-mean-square (RMS) of the signal-to-noise ratio (SNR) of ERRC. The SNR was computed on the grand mean of all subjects by dividing the MEG signal at each channel and time point by the standard deviation of the baseline. This provided a unified (magnetometers and gradiometers are combined together) and easy-to-interpret measure of sensor-level activity. Statistical significance was assessed with *t*-test from -.5s to 1 s after stimulus onset (FDR corrected for multiple comparisons, $p < .05$, Benjamini & Hochberg, 1995) on ERRC, separated for magnetometers and planar gradiometers (see Groppe, Urbach, & Kutas, 2011). We additionally imposed temporal (a minimum duration of 20 ms) as well as spatial (at least 2 concurrently significant channels) constraints on the reported results (for a similar procedure see, Bemis & Pylkkänen, 2011; Bemis & Pylkkänen, 2013; Zhang & Pylkkänen, 2015).

2.8. Source-level statistical analysis and visualization

Cortical responses to individual predictors (i.e., abstract semantic component, concrete semantic component, word frequency and word length; Figs. 2 to 5B) are illustrated as 20 ms averages of source-reconstructed brain activity thresholded to the 80 % of the local maxima at any given time-bin. Thus, this procedure is merely for localization purposes (for statistical comparison and the relative signal strength across the analyzed time-window, please refer to the sensor level statistics). We additionally imposed temporal (a minimum duration of 20 ms) as well as spatial (a minimum cluster size of 10 adjacent vertices) constraints on the reported results (for a similar procedure see, Bemis & Pylkkänen, 2011; Bemis & Pylkkänen, 2013; Zhang & Pylkkänen, 2015). Source-magnitude statistical maps for the comparison Concrete > Abstract (Fig. 6) were computed using whole-brain t-tests (two-tailed), on consecutive 100 ms average time windows (FDR corrected for multiple comparisons, $p < .05$, minimum number of 10 vertices). Contrary to previous source analysis, this contrast in source-space can be interpreted statistically and signal strength compared across timepoints.

3. Results

3.1. Behavioral results

Participants were instructed to categorize each stimulus as either related to sensory perception (i.e., they refer to something that can be easily perceived with the senses, like "red" and "telephone"), or unrelated to sensory perception (i.e., they refer to something that cannot easily be perceived with the senses, like "agreement" and "shame"). We expected participants to categorize relatively concrete words as related to sensory perception and relatively abstract words as unrelated to sensory perception. To assess this, we correlated participants' responses with the semantic principal components (see below). The results indicated a significant association between participants' responses (related

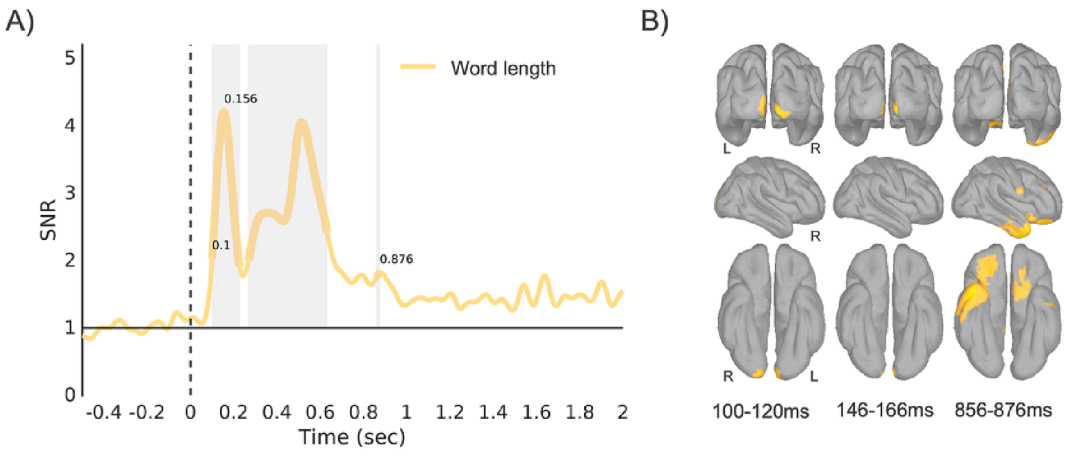


Fig. 2. Spatiotemporal dynamics of word length information encoding. A) Sensor-level results depicted as the root-mean-square of the SNR of ERRC of the word length predictor. Significant time intervals (FDR corrected, p <.05) are indicated with a thicker line and a shadowed gray area. 0 s = stimulus onset. B) Source-reconstructed maps of the word length predictor displayed as 20 ms time averages (threshold 80 % of local maxima, min cluster size 10, min duration 20 ms; for localization only) around the first significant time point (100–120 ms), the peak of activation (146–166 ms) and the last significant time point (856–876 ms).

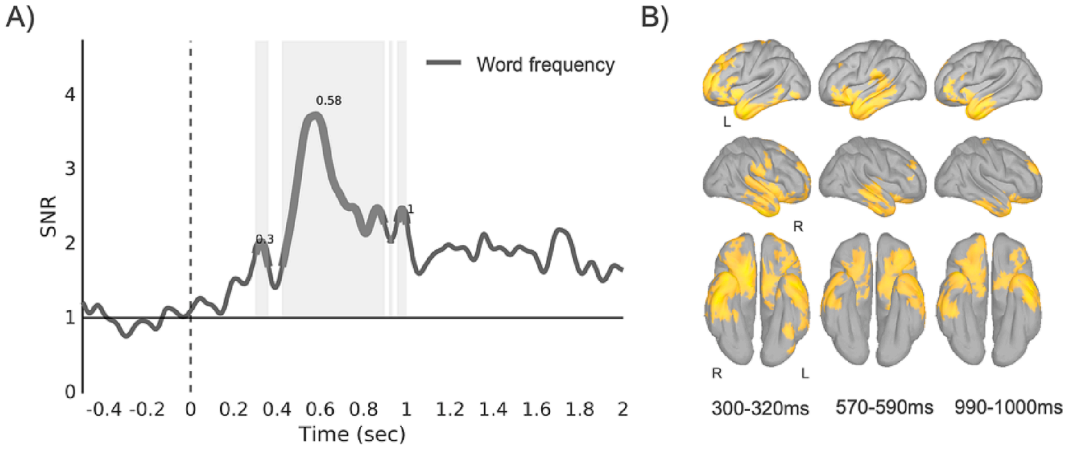


Fig. 3. Spatiotemporal dynamics of word frequency information encoding. A) Sensor-level results depicted as the root-mean-square of the SNR of ERRC of the word frequency predictor. Significant time intervals (FDR corrected, p <.05) are indicated with a thicker line and a shadowed gray area. 0 s = stimulus onset. B) Source-reconstructed maps of the word frequency predictor displayed as 20 ms time averages (threshold 80 % of local maxima, min cluster size 10, min duration 20 ms; for localization only) around the first significant time point (300–320 ms), the peak of activation (570–590 ms) and the last significant time point (990–1000 ms).

to sensory perception = 1, unrelated to sensory perception = 0) and our semantic dimensions (concrete semantic dimension: r(436) = 0.80, p <.001; abstract semantic dimension: r(436) = -0.23, p <.001). We did not analyze reaction times because participants' responses were delayed in order to avoid motion-related artifacts in the MEG signal (i.e., see Material and Methods for details).

3.2. Neural dynamics of lexical and semantic features

We first localized, in space and time, the encoding of the word length regressor (i.e., number of letters in a word). As predicted, this low-level visual information was encoded in and around primary visual cortices (bilaterally, Fig. 2B), starting approximately 100 ms after word appearance, peaking shortly after (SI Appendix, Figure S1) and remaining sustained up until 600 ms after word onset (see Fig. 2A). Such a highly predictable result served as a manipulation check for our source-localization procedure. At late time stages, word length information encoding saw the contribution of left inferior frontal and right anterior temporal and middle frontal brain systems.

Lexical access occurred shortly after processing of word-form related information. This is illustrated in Fig. 3A, where encoding of the word frequency predictor (Zipf; van Heuven et al., 2014) begins around 300 ms after visual word presentation, peaks at 580 ms and continues until one second after stimulus onset. Source-level results are illustrated in Fig. 3B. Encoding of information related to how frequent a word is in the language involves generators in the left ventral occipitotemporal cortex (approximately in the location of the Visual Word Form Area; Cohen et al., 2002) and anterior frontal brain regions. At the peak (approximately 600 ms after word onset), these encompassed inferior frontal, anterior temporal, middle temporal and superior temporal brain areas with an overall moderate left lateralization (see also SI Appendix, Figure S2/5). At later time points, the word frequency predictor was encoded in inferior frontal and anterior temporal brain areas, bilaterally (see Fig. 3B).

Abstract semantic information processing began approximately 300 ms after stimulus onset to peak 200 ms after (see Fig. 4A) and involved generators in prefrontal, inferior-frontal and anterior-temporal brain areas, bilaterally (see Fig. 4B).

Encoding of concrete semantic information showed transient responses in the 300 to 500 ms time window and a more sustained response from 600 ms to 1 s after stimulus onset (see Fig. 5A and SI Appendix, Fig. 4S). Source-level activation maps showed that concrete semantic information is encoded in prefrontal, inferior frontal and anterior temporal brain areas bilaterally (see Fig. 5B).

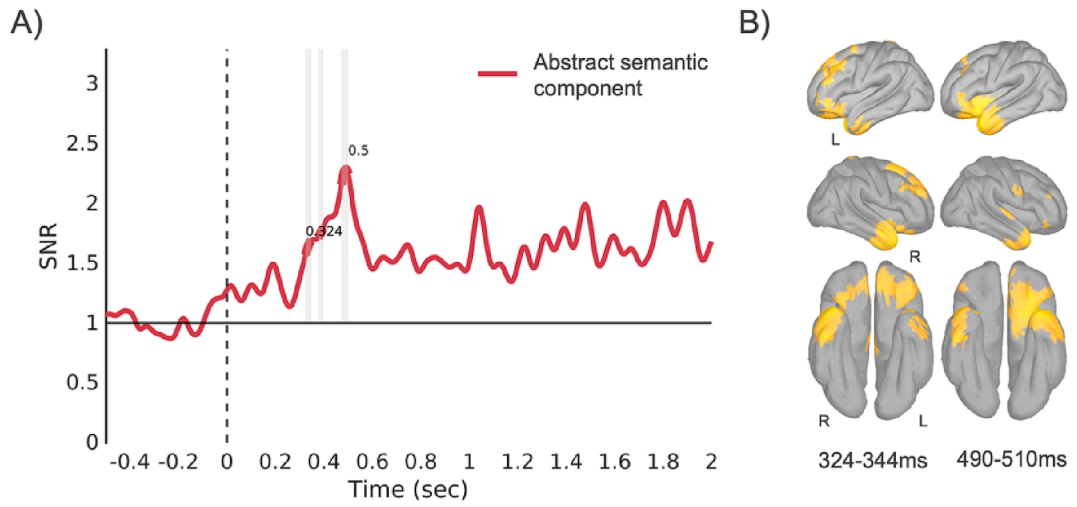


Fig. 4. Spatiotemporal dynamics of abstract semantic information encoding. A) Sensor-level results depicted as the root-mean-square of the SNR of ERRC of the abstract semantic component. Significant time intervals (FDR corrected, p <.05) are indicated with a thicker line and a shadowed gray area. 0 s = stimulus onset. B) Source-reconstructed maps of abstract semantic information encoding predictor displayed as 20 ms time averages (threshold 80 % of local maxima, min cluster size 10, min duration 20 ms; for localization only) around the first significant time point (324–344 ms) and the peak of activation (490–510 ms).

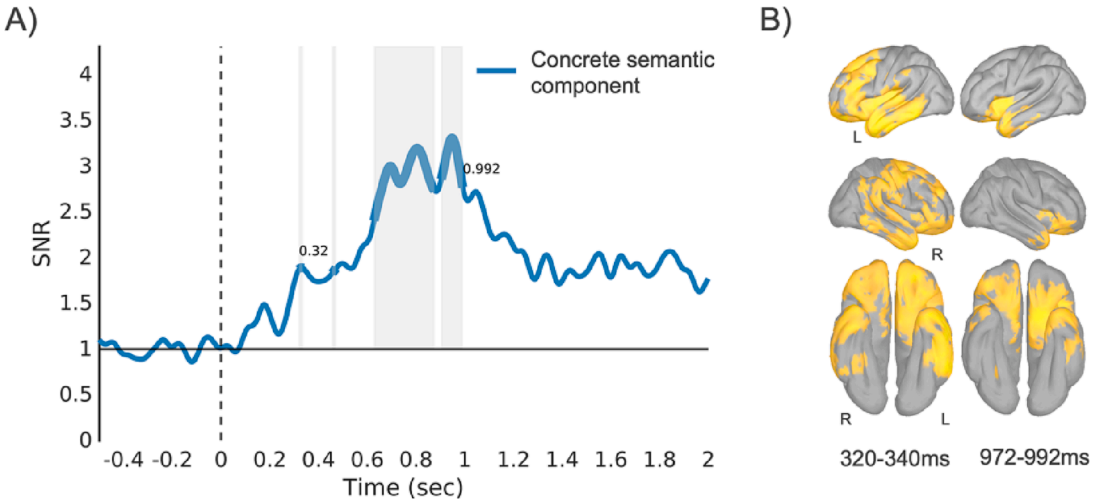


Fig. 5. Spatiotemporal dynamics of concrete semantic information encoding. A) Sensor-level results depicted as the root-mean-square of the SNR of ERRC of the concrete semantic component. Significant time intervals (FDR corrected, p <.05) are indicated with a thicker line and a shadowed gray area. 0 s = stimulus onset. B) Source-reconstructed maps of concrete semantic information encoding predictor displayed as 20 ms time averages (threshold 80 % of local maxima, min cluster size 10, min duration 20 ms; for localization only) around the first significant time point (320–340 ms) and the last significant time point (972–992 ms).

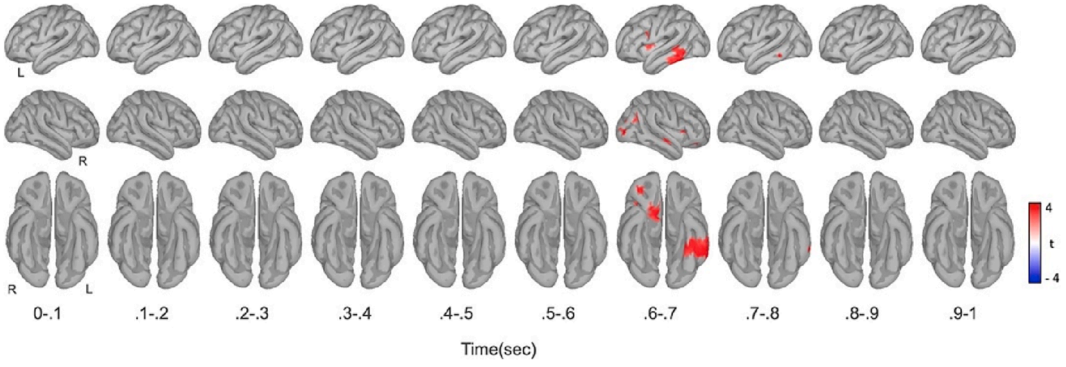


Fig. 6. Analysis of source-level magnitude activations. Source-reconstructed statistical maps of the contrast Concrete > Abstract (paired-sample *t*-test (two-tailed), FDR-corrected p <.05, min cluster size 10) in consecutive 100 ms average intervals.

Last, we investigated source-magnitude activity of abstract and concrete semantic regressors which allowed us to describe in statistical terms brain areas showing greater responses to one or the other type of information. Results are illustrated in Fig. 6 and evidenced greater activations for concrete semantic information in a distributed network of regions encompassing occipital, ventral occipito-temporal, inferior fusiform cortex and inferior-frontal brain areas approximately 700 ms after word presentation. In line with a dual-coding approach, no brain region showed a greater activation for abstract compared to concrete features.

4. Discussion

We took advantage of the high spatiotemporal resolution of MEG signals to test when and where abstract and concrete information is processed in the human brain. Using a multiple linear regression analysis of MEG-recorded brain activity, we obtained for every time point, channel, and subject event-related regression coefficients (ERRC) reflecting the contribution of each predictor to the data. Predictors of interest included variables associated with low-level visual information (the number of letters), lexical information (the frequency), as well as semantic properties (abstract and concrete feature dimensions) of each word.

Typically, the early stages of visual word recognition are dominated by the processing of low-level features (Carreiras, Armstrong, Perea, & Frost, 2014). This is illustrated in Fig. 2, where encoding of information related to the length of a word begins 100 ms after stimulus onset and peaks shortly after (for similar findings, see Dufau, Grainger, Midgley, & Holcomb, 2015; Hauk, Pulvermüller, Ford, Marslen-Wilson, & Davis, 2009). Source analysis localized this result in bilateral occipital areas, reflecting the visual nature of these early contributions (see also Dhond, Witzel, Dale, & Halgren, 2007; Hauk et al., 2009; Marinkovic et al., 2003). Sub-lexical information encoding was followed (~200 ms after) by lexico-semantic information encoding. That is, the word frequency predictor, the abstract semantic predictor, and the concrete semantic predictor all showed significant effects at around 300 ms after stimulus onset (see Figs. 3,4,5, A). The present findings reflect the cascade of underlying processes involved in visual word recognition (Grainger & Holcomb, 2009). A feedforward sweep of information cascades across sub-lexical and lexico-semantic stages resulting in parallel activations of lexical and semantic information approximately 300 ms after word presentation (for similar findings, see Chen, Davis, Pulvermüller, & Hauk, 2015; Halgren et al., 2002; Pylkkänen & Marantz, 2003). At these latencies, the processing of information related to word frequency involved frontotemporal and left ventral occipitotemporal brain areas, consistent with functional imaging results of reading material (see, for instance, Kronbichler et al., 2004; Schurz et al., 2010; Schuster, Hawelka, Hutzler, Kronbichler, & Richlan, 2016). Abstract and concrete semantic information processing, instead, involved a distributed network of brain areas encompassing both anterior frontal, anterior temporal and posterior brain areas (for similar findings, see Binder et al., 2009; Kana et al., 2012; Lambon-Ralph et al., 2017; Sabsevitz et al., 2005; Striem-Amit, Wang, Bi, & Caramazza, 2018; Wang et al., 2010).

Recent dual coding accounts of knowledge suggest that meaning is represented in the brain by a double code, which comprises language-derived representations in the (dorsal) ATL and sensory-derived representations in perceptual and motor regions (Bi, 2021). This approach further predicts that anterior temporal regions should encode both concrete and abstract features, whereas perceptual and motor regions (e.g., occipital cortex) should encode mostly concrete features. Our results are in keeping with this view and provide additional information with respect to the temporal dynamics possibly underlying this cognitive model: As illustrated in Figs. 4 and 5, encoding of both abstract and concrete semantic information showed early (300 ms after word onset) engagement of anterior temporal and inferior frontal brain areas, suggesting that representations of word's concreteness is not initially contingent on the activation of sensorimotor simulations or imagistic representations in perceptual and motor regions of the brain (Hauk, Davis, Ford, Pulvermüller, & Marslen-Wilson, 2006; Hultén et al., 2021). Moreover, source-level analysis contrasting the abstract and concrete semantic regressors revealed that: (i) there was no brain region that was activated more by abstract compared to concrete features, as predicted by DCT; (ii) fusiform and lateral occipitotemporal cortex, preferentially encode concrete semantic features over abstract ones, in keeping with the prediction of DCT; (iii) finally, this neural signature emerged relatively late, around 700 ms from word onset, suggesting a late activation of the sensorimotor/imagistic code during semantic processing.

Contrary to previous studies, a direct comparison of abstract and concrete semantic information encoding did not evidence stronger activations for abstract semantic information (see Fig. 6). Whereas this result is in line with DCT, which predicts no differences between abstract and concrete representation in linguistic coding, greater activations to abstract concepts as to concrete concepts were reported in the linguistic areas in the inferior frontal cortex and the anterior temporal lobe (see, for instance, Binder, Westbury, McKiernan, Possing, & Medler, 2005; Hoffman et al., 2015). Our results did not confirm these observations, and this discrepancy might be due to task-induced mechanisms. Whereas our semantic categorization task ("Was it a word related to the senses? YES - NO") put large emphasis on perceptual and motor representations of word meaning, several previous studies adopted tasks that emphasize linguistic properties of the stimuli (e.g., a lexical decision task, synonym judgment task; see for instance Binder et al., 2005; Hoffman et al., 2015). Wilson-Mendenhall, Simmons, Martin, and Barsalou (2013) showed that under task conditions which require deeper conceptual processing, the linguistic system did not show stronger engagement with abstract concepts as compared to concrete concepts, in line with our results. It is possible that language-related tasks show greater sensitivity to symbolic/linguistic representations of abstract words, inducing a greater activation for such items in the language/symbolic network (Wilson-Mendenhall et al., 2013). However, it is also possible that lexical decision or synonym judgment foster the processing of lexical-semantic features such as semantic diversity (Hoffman, Lambon Ralph, & Rogers, 2013), age of acquisition (Brown & Watson, 1987) or contextual availability (Schwanenflugel et al., 1988; Schwanenflugel & Stowe, 1989) which are often unbalanced between abstract and concrete words (abstract words usually have higher semantic diversity, lower contextual availability and are learned later in life). In this case, the higher activation of the language/symbolic network by abstract words could be due to the sensitivity of the network to such properties more than the preferential encoding of abstract semantic features per se.

Overall, the present findings suggest that contributions from a transmodal/linguistic code, housed in the perisylvian brain network, precede those of the imagistic/sensorimotor code in perceptual and motor regions, at least in the case of semantic concreteness. This result is in agreement with the language and situated simulation (LASS) theory (Barsalou, Santos, Simmons, & Wilson, 2008) which, assumes that contributions from the linguistic system precede those from the simulations system when a cue is a word, but different temporal profiles might emerge given different tasks and stimuli. The case of action verbs may be a paradigmatic one, with many studies showing an early (~200 ms) activation of primary motor regions (e.g., M1) in response to action verbs (Hauk et al., 2008; Pulvermüller, 2013; Pulvermüller, Shtyrov, & Ilmoniemi, 2005; van Elk, van Schie, Zwaan, & Bekkering, 2010). For instance, Garcia and colleagues (García et al., 2019), have recently shown that a machine learning classifier can distinguish action verbs (e.g., grasping) from nonaction verbs (e.g., sleeping), in M1, as early as 150 ms after word onset. Interestingly, the same classification was found in ATL, but only later, around 250–300 ms, thus revealing a reversed time course (sensorimotor regions before ATL) than the one we report here. Although their analyses were limited to these two regions of interest (ROIs), without control regions, and a limited number of participants, this data suggest that action verbs can activate simulations in

primary motor regions during the very early stages of word processing (actually, as early as the peak of activation we found in primary visual cortex for word length; Fig. 2).

However, taking into account the relevant exception of action verbs, in this experiment we showed that even when the task emphasized perceptual and motor representations of word meaning, posterior temporal and lateral occipital regions associated with a sensorimotor/imagistic code are preferentially activated by concrete features only during later stages of word processing. This finding supports the hypothesis that the concreteness advantage observed behaviorally during the early stages of word recognition can hardly be attributed to the activation of a sensorimotor/imagistic code in the sensorimotor regions of the brain (Bottini et al., 2021).

Dual code theories of knowledge in the brain successfully account for a large number of behavioral as well as neuroimaging findings (Bi, 2021; Paivio, 1986). Several aspects of this model, however, are still to be uncovered. It is for example unclear what is the exact nature of conceptual representations in the (dorsal) ATL. Is it really a language-based code that is "necessarily 'amodal,' 'symbolic' and independent from sensory experience" (Bi, 2021, p. 8)? In this view, the type of meaning supported by the linguistic code would be similar to the one encoded by current computational models in the field of natural language processing (NLP) and based on the distributional properties of words (Carota et al., 2017; Carota et al., 2021; Fernandino et al., 2016; Fernandino et al., 2022; Günther, Rinaldi, & Marelli, 2019). However, this state of affairs begs the actual question behind the grounding problem (Harnad, 1990; Shapiro, 2019): If the linguistic code is ultimately granted by links between word forms, how can they entail meaning in the sense of referring to something beyond other words? Under this assumption, if congenitally blind people could rely only on the amodal, ungrounded and sensory independent linguistic code to understand the meaning of "red" they would find themselves trapped in the Chinese Room (Searle, 1980). One possibility could be that, for blind people, the representation of highly-visual concepts in the ATL is still grounded, maybe onto dimensions of experience that are shared with non-visual concepts (e.g., intensity (glow vs. blaze), frequency (glow vs. twinkle); Bedny, Koster-Hale, Elli, Yazzolino, & Saxe, 2019) and therefore could be learned from the spared senses and applied by analogy to visual words. According to the same mechanism, visual concepts could be grounded onto emotional/affective dimensions (e.g., valence, arousal) that could for instance be easily applied to color knowledge (Osgood, 1952; Saysani, Corballis, & Corballis, 2021). This latter hypothesis would be consistent with the involvement of the dorsal ATL in color knowledge, on the basis of the role of this region in social and affective knowledge (Lambon-Ralph et al., 2017; Olson, McCoy, Klobusicky, & Ross, 2013). Moreover, it has been shown that abstract words, generally, are weighted more on social/affective dimensions compared to concrete words (Andrews, Frank, & Vigliocco, 2014; Kousta, Vigliocco, Vinson, Andrews, & Del Campo, 2011; Vigliocco, Kousta, Vinson, Andrews, & Del Campo, 2013), suggesting emotional grounding.

Another possible way to solve this problem is to focus on the link between the two codes. One such example is the "hub and spokes" model (H&S; Patterson, Nestor, & Rogers, 2007). H&S assumes that modality-specific sources of information (i.e., "spokes"), distributed across neocortical regions, encode different information sources (e.g., visual information in the occipital cortex, haptic in the sensorimotor cortex, linguistic in the perisylvian regions) that are integrated in the ATL "hub" (Lambon-Ralph et al., 2017; Patterson et al., 2007). In this model, the ATL is considered the home of transmodal representations that are not strictly language derived (language regions are one of the spokes in the model and simply one source of such integrated representations), but abstracted enough to affect all domains of knowledge (Damasio, 1989; Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Patterson & Erzinçlioğlu, 2008; Rogers & Patterson, 2007). Studies on functional connectivity corroborate this interpretation. By applying a graph-theoretic approach to the semantic brain network, Xu et al. (2017) highlighted two segregated systems for different types of semantic representations: a multimodal experiential content system in the default mode network and language supported content system in the perisylvian brain network. In this framework, anterior temporal areas are not the house to either linguistic or sensorimotor representations but are where these two representations converge (Xu et al., 2017). It has been also proposed that the ATL hub is organized according to a gradient of abstractness: The dorsal ATL would be more active for abstract concepts, given its preferential connectivity with perisylvian language regions; Whereas the ventro-medial ATL would be more active for concrete concepts given its connections with visual brain regions. However, the spatial resolution of MEG is limited and makes the distinction between subparts of the ATL difficult to achieve. Furthermore, our design does not allow to disentangle whether linguistic, or transmodal representations (or both) encoded abstract and concrete semantic features in anterior temporal regions.

5. Conclusions

To conclude, the present findings shed new light on the spatiotemporal dynamics of abstract and concrete semantic representations in the brain. At early processing stages, abstract and concrete semantic information encoding was underpinned by common neural substrates in the anterior temporal lobe, whereas at later latencies, occipito-temporal regions showed preferential responses to concrete information only. We suggest that concreteness is encoded in the brain via the early contribution of a transmodal/linguistic code (housed in frontotemporal brain systems), followed by the activation of an imagistic/sensorimotor code in perceptual regions. Results are broadly consistent with a dual-coding approach, although the strictly linguistic nature of ATL representations remains putative and waits for further empirical studies.

CRediT authorship contribution statement

Lorenzo Vignali: Conceptualization, Data curation, Formal analysis, Investigation, Software, Methodology, Visualization, Writing – original draft. **Yangwen Xu:** Conceptualization, Formal analysis, Writing – review & editing. **Jacopo Turini:** Investigation, Resources, Data curation. **Olivier Collignon:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition. **Davide Crepaldi:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition. **Roberto Bottini:** Conceptualization, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.bandl.2023.105298.

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