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20	Abstract
21 22 23 24 25	Dual coding theories of knowledge suggest that meaning is represented in the brain by a double code, which comprises language-derived representations in the Anterior Temporal Lobe and sensory-derived representations in perceptual and motor regions. This approach predicts that concrete semantic features should activate both codes, whereas abstract features rely exclusively on the linguistic code. Using magnetoencephalography (MEG), we adopted a temporally resolved multiple regression approach to

identify the contribution of abstract and concrete semantic predictors to the underlying brain signal. Results evidenced early involvement of anterior-temporal and inferior-frontal brain areas in both abstract and concrete semantic information encoding. At later stages, occipito-temporal regions showed greater responses to concrete compared to abstract features. The present findings shed new light on the temporal dynamics of abstract and concrete semantic representations in the brain and suggest that the concreteness of words processed first with a transmodal/linguistic code, housed in frontotemporal brain systems, and only after with an imagistic/sensorimotor code in perceptual and motor regions.

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34 Keywords

35 Abstract, concrete, dual-code, semantic, magnetoencephalography, encoding, semantic features

36 1. Introduction

Abstract and concrete semantic representations form fundamental aspects of word meaning. For instance,
concrete features (e.g., four legs, red fur), as well as abstract features (e.g., intelligent, aggressive),
contribute to the representation of a fox in semantic knowledge (Borghesani & Piazza, 2017; Smith et al.,
1974). 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.

42 To explain how various sorts of knowledge guide a broad range of behaviors, Dual Coding Theories 43 (DCT: Paivio, 1986, 1991) put forward the idea that, in the brain, semantic knowledge is represented in a 44 dual coding system comprising a linguistic code, and an imagistic/sensorimotor code. In DCT, abstract and 45 concrete concepts can both be represented through the linguistic code, whereas the imagistic/sensorimotor code is available only for concrete aspects of meaning. In experimental psychology, the fact that concrete 46 47 words are recognized faster (Kroll & Merves, 1986; Schwanenflugel et al., 1988; Schwanenflugel & Stowe, 48 1989) and memorized better (Allen & Hulme, 2006; de Groot, 1989; Fliessbach et al., 2006) than abstract words (i.e., the concreteness effect) has been traditionally taken as evidence in favor of the dual coding 49 50 approach: only concrete concepts can activate both codes (linguistic and sensorimotor), a condition which 51 gives them a processing advantage (Connell & Lynott, 2012; Paivio, 1986). However, the study of the 52 concreteness effect in congenitally blind people has cast doubts on this interpretation (Bottini et al., 2021). 53 Despite lacking a sensory code for visual features, early blind people processed visual unimodal-concrete 54 words (e.g., "red," "multicolor," "transparent") faster than abstract words, showing a concreteness effect that 55 was indistinguishable from the one of sighted people (Bottini et al., 2021) and suggesting that the 56 concreteness advantage is not driven by the availability of a double code for concrete words.

57 If, on the one hand, the study of blind people has shaken the confidence in psychological evidence 58 considered a hallmark of dual coding models, on the other hand, it has revived the interest in DCTs from a 59 neuro-cognitive perspective. Are sensory-derived and non-sensory-derived representations encoded in 60 dissociable brain codes? A recent line of studies exploring the brain basis of visual knowledge in the 61 absence of vision has provided alternative neurocognitive evidence for a dual code of semantic knowledge 62 in the brain (see Bi, 2021). Two studies focusing on color representations in sighted and congenitally blind 63 have shown that posterior brain areas in the V4 complex encode the similarity of color words, but only in 64 sighted people. However, color similarity is also encoded in the dorsal anterior temporal lobe (ATL) in both 65 sighted and blind (Bottini et al., 2020; X. Wang et al., 2020). Thus, the dorsal ATL seems to provide a non-66 sensory code to represent knowledge, both concrete and abstract, whereas a perceptual code for concrete 67 representations relies on posterior perceptual regions and may not be available in the case of sensory 68 deprivation (Bi, 2021).

69 Beyond research with populations devoid of specific aspects of perceptual experience, functional 70 resonance imaging (fMRI) studies investigating topological as well as functional properties of the semantic 71 network provide additional evidence in favor of a dual-code account of semantic knowledge in the brain 72 (e.g., Bi, 2021; Xu et al., 2017). From a network perspective, the dorsal anterior temporal lobe (dATL) and 73 posterior sensory and motor regions are components of dissociable brain systems. The dATL belongs to 74 the high-level linguistic system in the left perisylvian network, encompassing the inferior frontal gyrus, the 75 lateral temporal cortex, and the inferior parietal cortex (for instance, Fedorenko et al., 2011; Friederici, 76 2011). It has stronger connections to the other regions in the language network than the sensorimotor 77 regions(Jackson et al., 2016; X. Wang et al., 2020). The left perisylvian language network is consistently 78 activated in semantic tasks (Binder et al., 2009; Xu et al., 2017), and is considered to play a role in 79 language-supported semantic processing (Xu et al., 2017). Beyond DCTs, other models suggest that both 80 codes are present in the ATL, arranged in a continuous transmodal gradient (e.g., Lambon-Ralph et al., 81 2017). That is, the ATL is considered a transmodal/graded hub with a linguistic neural code in its dorsal part, and a perceptual code in its ventral part (Hoffman et al., 2015; Visser & Lambon Ralph, 2011). 82

83 On the contrary, visual regions (including the color region V4) belong to the highly distributed 84 sensorimotor brain system, (see Wang et al., 2020) which reflects relevant perceptual dimensions of the input such as visual, tactile, auditory, etc. (Barsalou et al., 2003; Binder et al., 2005, 2009; Binder & Desai, 85 2011; Hoffman et al., 2015; Kana et al., 2012; Sabsevitz et al., 2005). These regions are usually more active 86 87 for concrete compared to abstract concepts (Binder et al., 2005, 2009; Binder & Desai, 2011; J. Wang et 88 al., 2010) and may host sensorimotor simulations of perceptual referents during semantic processing. 89 However, as fMRI suffers from poor temporal resolution, several questions about the spatiotemporal 90 dynamics of the dual code of knowledge in the brain remain unanswered. For instance, it is unclear whether 91 transmodal/language-derived representations in the ATL are activated before, after, or at the same time as 92 sensorimotor representations in perceptual regions. This missing information is crucial to understand the 93 neural dynamics of conceptual processing and, in particular, how concreteness (abstractness) is encoded 94 in the brain.

95 To answer these questions, we took advantage of the high temporal resolution of 96 magnetoencephalography (MEG) signals combined with source-reconstruction techniques to assess the 97 spatiotemporal dynamics of abstract and concrete semantic representations. Forty-six participants 98 performed a semantic categorization task on 438 written words. Each word referred to a concept (e.g., 99 chair, dog, policeman) that was independently rated across 65 feature dimensions (e.g., color, shape, 100 happiness, arousal, cognition, etc.; Binder et al. 2016). Using principal component analysis (PCA), we 101 reduced the dimensionality of this feature space into one abstract and one concrete semantic principal 102 component. We then used a combination of multiple linear regression analysis and source reconstruction 103 methods to assess neural dynamics of abstract and concrete semantic representations while keeping into 104 account other types of psycholinguistic information processed during visual word recognition.

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106 2. Material and Methods

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108 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.

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115 2.2. Experimental design

116 We derived our stimulus set from a previous work by Binder and colleagues (Binder et al., 2016). 117 Out of 535 English words filed in Binder et al.'s (2016) original work, 438 were translated into Italian (352 118 nouns in the singular form, 54 verbs in the infinite tense, and 32 adjectives in the singular masculine form). 119 Selected words could be unambiguously translated into Italian. Participants were instructed to categorize 120 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 121 122 whiteboard (1440x1080 pixel resolution) using a ProPixx DLP projector (VPixxTechnologies, Canada) at a 123 120 Hz refresh rate. Stimulus presentation was controlled via Psychtoolbox (Kleiner et al., 2007) running in 124 a MATLAB 2015a environment. At the beginning of each trial, a 1s blank screen followed by a 0.5s fixation 125 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 0.3s, followed by a 1.7s 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 2s and was followed by an interstimulus interval randomly jittered between 0.3s and
0.6s. 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 hours and

- 133 was divided into twelve seven-minutes runs separated by eleven short breaks and one 30 min break.
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135 2.3. *MEG Data acquisition and preprocessing*

MEG data were recorded using a whole-head 306 sensor (204 planar gradiometers; 102 magnetometers) Vector-view system (Elekta Neuromag, Helsinki, Finland). Five head-position indicator coils (HPIs) were used to continuously determine the head position with respect to the MEG helmet. MEG signals were recorded at a sampling rate of 1 kHz and an online band-pass filtered between 0.1 and 300 Hz. At the beginning of each experimental session, fiducial points of the head (the nasion and the left and right pre-auricular points) and a minimum of 300 other head-shape samples were digitized using a Polhemus FASTRAK 3D digitizer (Fastrak Polhemus, Inc., Colchester, VA, USA).

143 The raw data were processed using MaxFilter 2.0 (Elekta Neuromag ®). First, bad channels 144 (identified via visual inspection) were replaced by interpolation. External sources of noise were separated 145 from head-generated signals using a spatio-temporal variant of signal-space separation (SSS). Last, 146 movement compensation was applied, and each run was aligned to an average head position. All further 147 analysis steps were performed in MATLAB 2019a using non-commercial software packages such as 148 Fieldtrip (Oostenveld et al., 2011), Brainstorm (Tadel et al., 2011) and custom scripts. Continuous MEG 149 recordings were filtered at 0.1 Hz using a two-pass Butterworth high-pass filter and epoched from -1.5 s 150 before to 2s after stimulus onset. Time segments contaminated by artifacts were manually rejected (total 151 data loss of M = 2.4% SD = 1.8%). A Butterworth low-pass filter at 40Hz was applied to the epoched data. 152 Before encoding, each trial segment was baseline corrected with respect to a -500 to -100ms time window 153 before stimulus onset.

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155 2.4. Multiple linear regression analysis

156 Multiple linear regression analysis was applied to MEG data following the approach used in 157 previous M/EEG studies (Chen et al., 2013, 2015; Hauk et al., 2006, 2009; Miozzo et al., 2015). The solution 158 of a multiple regression provides the best least-square fit of all variables simultaneously to the data (Bertero 159 et al., 1985). For each time point, channel and subject we calculated event-related regression coefficients 160 (ERRCs) reflecting the contribution of each predictor to the MEG signal. We focused on four predictors 161 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 162 163 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 164 165 orthogonalized via varimax rotation. Before encoding the predictors of each model were converted to 166 normalized z-scores and tested for multicollinearity using a condition number test (Belsley, 1982). The 167 output of the test is a condition index, which in the present study never exceeded a threshold of 2 (with test 168 values < 6 collinearity is not seen as a problem).

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170 2.5. Predictor variables

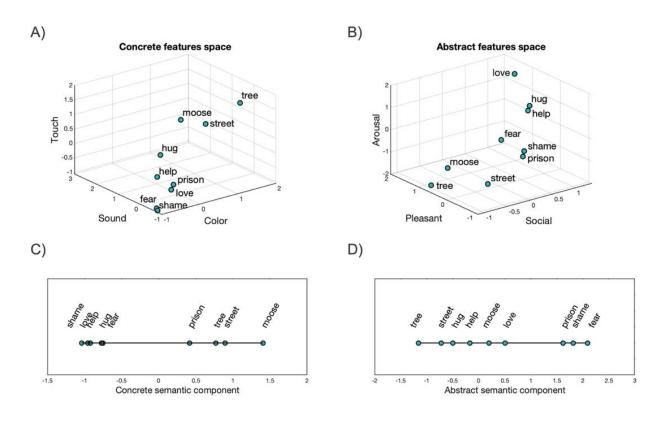
171 The aim of the present study was to investigate the contribution of abstract and concrete semantic 172 dimensions of knowledge to concepts representations. On this account, we derived our stimulus set from a 173 previous work by Binder and colleagues (Binder et al., 2016). These authors collected ratings of the 174 salience of 65 biologically plausible features to word meaning (for a detailed description of the procedure 175 see Binder et al. 2016). For every word in the database (e.g., lemon), more than one thousand participants 176 were asked to rate how each of the features (e.g., color) was associated with that aspect of the experience 177 (e.g., would you define a lemon as having a characteristic or defining color?). The result is a semantic space 178 where concepts can be represented as single entities into a multidimensional space having perceptual (e.g., 179 sound, shape, smell) and conceptual (e.g., arousal, social, sad) features as dimensions. Crucially, features 180 spanned both abstract and concrete domains of conceptual knowledge thus represent an ideal framework 181 to operationalize our assumptions.

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183 2.5.1. Semantic components

184 As mentioned above, more than sixty features composed our semantic space. Encoding the entire 185 space in one single model, however, would be suboptimal. In fact, features are highly intercorrelated with 186 each other, leaving us with a multicollinearity issue. One way this can be avoided is through dimensionality 187 reduction techniques (Cunningham & Yu, 2014), such as principal component analysis (PCA). PCA generates a series of principal components (PCs) representing the same data in a new coordinate system, 188 189 with the first PC usually accounting for the largest percentage of data variance. Following the concrete 190 versus abstract labeling provided in the original database (Binder et al., 2016), we separated the entire 191 semantic space (65-features) into concrete features (N = 31, encompassing Vision, Somatic, Audition 192 Gustation, Olfaction and Motor domains) and abstract features (N = 31, encompassing Spatial, Temporal, 193 Causal, Social, Emotion, Drive and Attention domains). Three features (i.e., Complexity, Practice, Caused) 194 were excluded due to incomplete ratings. Thus, each word could be considered as a point in a concrete 195 semantic features' space (see Figure 1A), and in an abstract semantic features' space (see Figure 1B). We 196 used PCA to reduce the dimensionality of the dataset and adopted the first concrete semantic component 197 (Figure 1C; 24.7% of variance explained) and the first abstract semantic component (Figure 1D; 27.4% of 198 the variance explained), to represent the same data in a new one-dimensional coordinate system. 199 Importantly, the resulting semantic components do not simply reflect how concrete and how abstract a word 200 is, but instead represents concrete and abstract aspects of concepts in a new low-dimensional space that 201 encodes the most salient structural features of the high-dimensional space from which it is derived. For 202 instance, in the concrete principal component, "moose" is more similar to "street" than to "hug", whereas 203 the opposite is true in the abstract principal component (Figure 1, C-D).

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Figure 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.

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214 2.5.2. Linguistic features

For each of the selected words, we obtained psycholinguistic features: Word Frequency (in Zipf's scale, M = 4, SD = 0.8; van Heuven et al. 2014) was calculated as the frequency of occurrence of a given word in a large corpus of text samples (SUBTLEX-IT; Crepaldi et al. 2015). Word length was encoded as the number of letters of each word (M = 6.9, SD = 1.6).

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220 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 3T scanner (Siemens, Erlangen, Germany) using a 3D MPRAGE sequence, 1-mm³ resolution, TR = 2140ms, TI = 900ms, TE = 2.9ms, flip angle 12°. 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

227 surfaces was based on ~300 scalp surface locations. When no individual MRI was available (6 participants), 228 we warped participants' head shapes to a standard ICBM152 brain template. The data noise covariance 229 matrix was calculated from the baseline interval (-500ms to -100ms) of the different trials. The forward 230 model was obtained using the overlapping spheres method (Huang et al., 1999) as implemented in the 231 Brainstorm software. We then: i) Estimated current density maps for event-related regression coefficients 232 onto a 15000 vertices boundary element. Dipole sources were assumed to be perpendicular to the cortical 233 surface. ii) Normalized current density values with respect to a -500ms to -100ms baseline period (z-234 transform). iii) Rectified current density values (converted to absolute values). iv) Spatially smoothed the 235 source maps using an 8mm full width at half the maximum smoothing parameter (FWHM) and, finally, v) 236 the individual results were projected to a default template (ICBM152).

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238 2.7. Sensor-level statistical analysis and visualization

239 In line with previous studies (Chen et al., 2013, 2015; Hauk et al., 2006, 2009; Miozzo et al., 2015), 240 we depicted the time course of different regressors as the root-mean-square (RMS) of the signal-to-noise 241 ratio (SNR) of ERRC. The SNR was computed on the grand mean of all subjects by dividing the MEG signal 242 at each channel and time point by the standard deviation of the baseline. This provided a unified 243 (magnetometers and gradiometers are combined together) and easy-to-interpret measure of sensor-level 244 activity. Statistical significance was assessed with t-test from -.5s to 1s after stimulus onset (FDR corrected 245 for multiple comparisons, p < .05, Benjamini & Hochberg, 1995) on ERRC, separated for magnetometers 246 and planar gradiometers (see Groppe et al., 2011). We additionally imposed temporal (a minimum duration 247 of 20ms) as well as spatial (at least 2 concurrently significant channels) constraints on the reported results.

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249 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; Figures 2 to 5, B) are illustrated as 20ms averages of sourcereconstructed brain activity thresholded to the 80% of the local maxima. We additionally imposed temporal (a minimum duration of 20ms) as well as spatial (a minimum cluster size of 10 adjacent vertices) constraints on the reported results. Source-magnitude statistical maps (i.e., Concrete > Abstract, Figure 6) were computed using whole-brain t-tests (two-tailed), on consecutive 100ms average time windows (FDR corrected for multiple comparisons, p < .05, minimum number of 10 vertices).

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258 3. Results

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260 3.1. Behavioral results

261 Participants were instructed to categorize each stimulus as either related to sensory perception 262 (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 263 264 senses, like "agreement" and "shame"). We expected participants to categorize relatively concrete words 265 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 266 267 results indicated a significant association between participants' responses and our semantic dimensions 268 (concrete semantic dimension: r(436) = .80, p < .001; abstract semantic dimension: r(436) = -.23, p < .001).

We did not analyze reaction times because participants' responses were delayed in order to avoid motionrelated artifacts in the MEG signal (i.e., see Material and Methods for details).

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272 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, Figure 2B), starting approximately 100ms after word appearance, peaking shortly after and remaining sustained up until 600ms after word onset (see Figure 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.



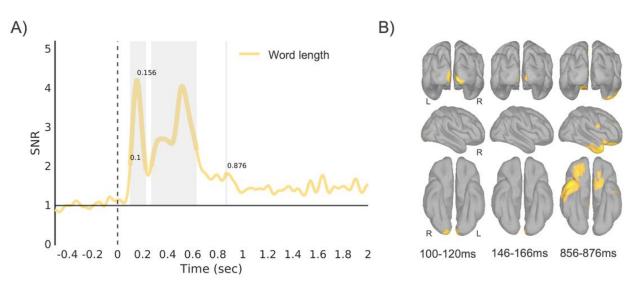




Figure 2. Spatiotemporal dynamics of word length information encoding. A) Sensor-level results depicted as the root-meansquare of the SNR of ERRC of the word length predictor. Significant time intervals (FDR corrected, p < .05) are indicated with a thicker line and a shadowed gray area. 0s = stimulus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

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288 Lexical access occurred shortly after processing of word-form related information. This is illustrated 289 in Figure 3A, where encoding of the word frequency predictor (Zipf; van Heuven et al. 2014) begins around 290 300ms after visual word presentation, peaks at 580ms and continues until one second after stimulus onset. 291 Source-level results are illustrated in Figure 3B. Encoding of information related to how frequent a word is 292 in the language involves generators in the left ventral occipitotemporal cortex (approximately in the location 293 of the Visual Word Form Area; Cohen et al. 2002) and anterior frontal brain regions. At the peak 294 (approximately 600ms after word onset), these encompassed inferior frontal, anterior temporal, middle 295 temporal and superior temporal brain areas with an overall moderate left lateralization. At later time points, 296 the word frequency predictor was encoded in inferior frontal and anterior temporal brain areas, bilaterally 297 (see Figure 3B).

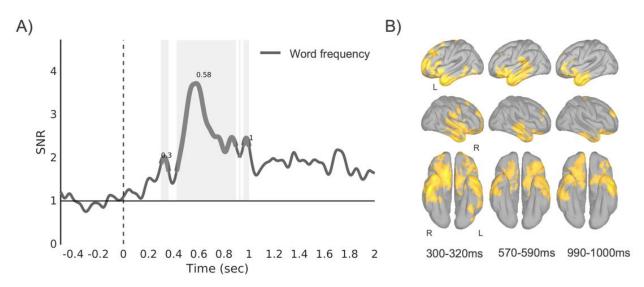
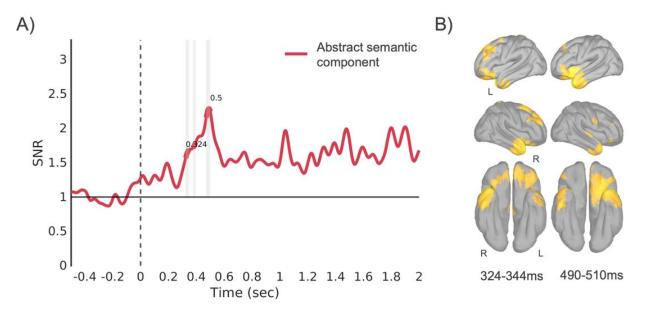


Figure 3. Spatiotemporal dynamics of word frequency information encoding. A) Sensor-level results depicted as the rootmean-square of the SNR of ERRC of the word frequency predictor. Significant time intervals (FDR corrected, p < .05) are indicated with a thicker line and a shadowed gray area. 0s = stimulus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

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



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Figure 4. Spatiotemporal dynamics of abstract semantic information encoding. A) Sensor-level results depicted as the rootmean-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. 0s = stimulus onset. B) Source-reconstructed maps of abstract semantic information encoding predictor displayed as 20ms time averages (threshold 80% of local maxima, min cluster size 10, min duration 20ms) around the first significant time point (324-344ms) and the peak of activation (490-510ms).

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

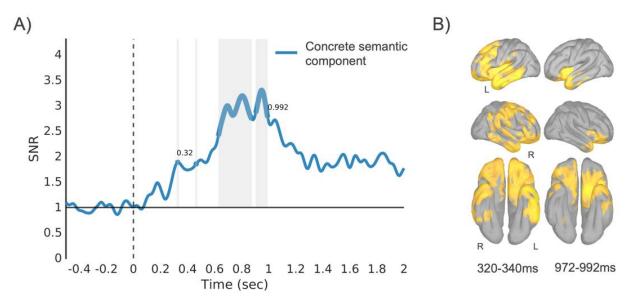
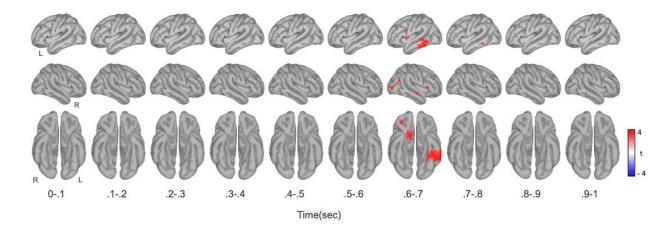




Figure 5. Spatiotemporal dynamics of concrete semantic information encoding. A) Sensor-level results depicted as the rootmean-square of the SNR of ERRC of the concrete semantic component. Significant time intervals (FDR corrected, p < .05) are indicated with a thicker line and a shadowed gray area. 0s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

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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 Figure 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 700ms after word presentation. In line with a dual-coding approach, no brain region showed a greater activation for abstract compared to concrete features.



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Figure 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 100ms average intervals.

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340 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 eventrelated 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.

348 Typically, the early stages of visual word recognition are dominated by the processing of low-level features (Carreiras et al., 2014). This is illustrated in Figure 2, where encoding of information related to the 349 350 length of a word begins 100ms after stimulus onset and peaks shortly after (for similar findings, see Dufau 351 et al., 2015; Hauk et al., 2009). Source analysis localized this result in bilateral occipital areas, reflecting 352 the visual nature of these early contributions (see also Dhond et al., 2007; Hauk et al., 2009; Marinkovic et 353 al., 2003). Sub-lexical information encoding was followed (~200ms after) by lexico-semantic information 354 encoding. That is, the word frequency predictor, the abstract semantic predictor, and the concrete semantic predictor all showed significant effects at around 300ms after stimulus onset (see Figures 3-4-5, A). The 355 356 present findings reflect the cascade of underlying processes involved in visual word recognition (Grainger 357 & Holcomb, 2009). A feedforward sweep of information cascades across sub-lexical and lexico-semantic 358 stages resulting in parallel activations of lexical and semantic information approximately 300ms after word 359 presentation (for similar findings, see Chen et al., 2015; Halgren et al., 2002; Pylkkänen & Marantz, 2003). 360 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 361 instance, Kronbichler et al., 2004; Schurz et al., 2010; Schuster et al., 2016). Abstract and concrete 362 semantic information processing, instead, involved a distributed network of brain areas encompassing both 363 364 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 et al., 2018; J. Wang et
al., 2010).

367 Recent dual coding accounts of knowledge suggest that meaning is represented in the brain by a 368 double code, which comprises language-derived representations in the (dorsal) ATL and sensory-derived 369 representations in perceptual and motor regions (Bi, 2021). This approach further predicts that anterior 370 temporal regions should encode both concrete and abstract features, whereas perceptual and motor 371 regions (e.g., occipital cortex) should encode mostly concrete features. Our results are in keeping with this 372 view and provide additional information with respect to the temporal dynamics possibly underlying this 373 cognitive model: As illustrated in Figures 4 and 5, encoding of both abstract and concrete semantic 374 information showed early (300ms after word onset) engagement of anterior temporal and inferior frontal 375 brain areas, suggesting that representations of word's concreteness is not initially contingent on the 376 activation of sensorimotor simulations or imagistic representations in perceptual and motor regions of the 377 brain (Hauk et al., 2006; Hultén et al., 2021). Moreover, source-level analysis contrasting the abstract and 378 concrete semantic regressors revealed that: (i) there was no brain region that was activated more by 379 abstract compared to concrete features, as predicted by DCT; (ii) fusiform, lateral occipitotemporal, 380 precentral and orbitofrontal regions preferentially encode concrete semantic features over abstract ones, 381 in keeping with the prediction of DCT; (iii) finally, this neural signature emerged relatively late, around 382 700ms from word onset, suggesting a late activation of the sensorimotor/imagistic code during semantic 383 processing.

384 Contrary to previous studies, a direct comparison of abstract and concrete semantic information 385 encoding did not evidence stronger activations to abstract semantic information (see Figure 6). Whereas 386 this result is in line with DCT, which predicts no differences between abstract and concrete representation 387 in linguistic coding, greater activations to abstract concepts as to concrete concepts were reported in the 388 linguistic areas in the inferior frontal cortex and the anterior temporal lobe (see, for instance, Binder et al., 389 2005; Hoffman et al., 2015). Our results did not confirm these observations, and this discrepancy might be 390 due to task-induced mechanisms. Whereas our semantic categorization task ("Was it a word related to the 391 senses? YES - NO") put large emphasis on perceptual and motor representations of word meaning, several 392 previous studies adopted tasks that emphasize linguistic properties of the stimuli (e.g., a lexical decision 393 task, synonym judgment task; see for instance Binder et al., 2005; Hoffman et al., 2015). Wilson-394 Mendenhall et al. (2013) showed that under task conditions which require deeper conceptual processing, 395 the linguistic system did not show stronger engagement with abstract concepts as compared to concrete 396 concepts, in line with our results. It is possible that language-related tasks show greater sensitivity to 397 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 398 399 decision or synonym judgment foster the processing of lexical-semantic features such as semantic diversity 400 (Hoffman et al., 2013), age of acquisition (Brown & Watson, 1987) or contextual availability 401 (Schwanenflugel et al., 1988; Schwanenflugel & Stowe, 1989) which are often unbalanced between 402 abstract and concrete words (abstract words usually have higher semantic diversity, lower contextual 403 availability and are learned later in life). In this case, the higher activation of the language/symbolic network 404 by abstract words could be due to the sensitivity of the network to such properties more than the preferential 405 encoding of abstract semantic features per se.

406 Overall, the present findings suggest that contributions from a transmodal/linguistic code, housed 407 in the perisylvian brain network, precede those of the imagistic/sensorimotor code in perceptual and motor 408 regions, at least in the case of semantic concreteness. We cannot, however, exclude the prospect that, 409 under different circumstances, this sequence of events would unfold differently. The case of action verbs 410 may be a paradigmatic one, with many studies showing an early (~200ms) activation of primary motor

regions (e.g., M1) in response to action verbs (Hauk et al., 2008; Pulvermüller, 2013; Pulvermüller et al., 411 412 2005; van Elk et al., 2010). For instance, Garcia and colleagues (García et al., 2019), have recently shown 413 that a machine learning classifier can distinguish action verbs (e.g., grasping) from nonaction verbs (e.g., 414 sleeping), in M1, as early as 150ms after word onset. Interestingly, the same classification was found in 415 ATL, but only later, around 250-300ms, thus revealing a reversed time course (sensorimotor regions before 416 ATL) than the one we report here. Although their analyses were limited to these two regions of interest 417 (ROIs), without control regions, and a limited number of participants, this data suggest that action verbs 418 can activate simulations in primary motor regions during the very early stages of word processing (actually, 419 as early as the peak of activation we found in primary visual cortex for word length; Figure 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, lateral occipital and precentral 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).

427 Dual code theories of knowledge in the brain successfully account for a large number of behavioral 428 as well as neuroimaging findings (Bi, 2021; Paivio, 1986). Several aspects of this model, however, are still 429 to be uncovered. It is for example unclear what is the exact nature of conceptual representations in the 430 (dorsal) ATL? Is it really a language-based code that is "necessarily 'amodal,' 'symbolic' and independent 431 from sensory experience" (Bi, 2021, p. 8)? In this view, the type of meaning supported by the linguistic code 432 would be similar to the one encoded by current computational models in the field of natural language 433 processing (NLP) and based on the statistical relationships with other words in speech (for a review Günther 434 et al., 2019). In other words, the meaning is supported in language contexts (Barsalou et al., 2008; Vigliocco 435 et al., 2009; Xu et al., 2017). However, this state of affairs begs the actual question behind the grounding 436 problem (Harnad, 1990): If the linguistic code is ultimately granted by links between word forms, how can 437 they entail meaning in the sense of referring to something beyond other words? Under this assumption, if 438 congenitally blind people could rely only on the amodal, ungrounded and sensory independent linguistic 439 code to understand the meaning of "red" they would find themselves trapped in the Chinese Room (Searle, 440 1980).

441 To solve this problem, several influential theories focus on the link between the two codes. One 442 such example is "hub and spokes mode (H&S; Patterson et al., 2007). H&S assumes that modality-specific 443 sources of information (i.e., "spokes"), distributed across neocortical regions, encode different information 444 sources (e.g., visual information in the occipital cortex, haptic in the sensorimotor cortex, linguistic in the 445 perisvlvian 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 446 447 derived (language regions are one of the spokes in the model and simply one source of such integrated 448 representations) but abstracted enough to affect all domains of knowledge (A. R. Damasio, 1989; H. 449 Damasio et al., 1996; Patterson & Erzinclioğlu, 2008; Rogers & Patterson, 2007). Studies on functional 450 connectivity corroborate this interpretation. By applying a graph-theoretic approach to the semantic brain 451 network, Xu et al. (2017) highlighted two segregated systems for different types of semantic 452 representations: a multimodal experiential content system in the default mode network and language 453 supported content system in the perisylvian brain network. In this framework, anterior temporal areas are 454 not the house to either linguistic or sensorimotor representations but are where these two representations 455 converge (Xu et al., 2017). It has been also proposed that the ATL hub is organized according to a gradient 456 of abstractness: The dorsal ATL would be more active for abstract concepts, given its preferential

457 connectivity with perisylvian language regions; Whereas the ventro-medial ATL would be more active for
 458 concrete concepts given its connections with visual brain regions. However, the spatial resolution of MEG

459 is limited and makes the distinction between subparts of the ATL difficult to achieve. Finally, our design,

460 does not allow to disentangle whether linguistic, or integrated representations (or both) encoded abstract

- 461 and concrete semantic features in anterior temporal regions.
- 462

463 5. Conclusions

464 To conclude, the present findings shed new light on the spatiotemporal dynamics of abstract and concrete 465 semantic representations in the brain. At early processing stages, abstract and concrete semantic 466 information encoding was underpinned by common neural substrates in the anterior temporal lobe, whereas at later latencies, sensory-motor areas showed preferential responses to concrete information only. We 467 468 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 469 470 perceptual regions. Results are broadly consistent with a dual-coding approach, although the strictly 471 linguistic nature of ATL representations remains putative and waits for further empirical studies.

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473 Author contributions

L. Vignali: Conceptualization, Data curation, Formal analysis, Investigation, Software,
Methodology, Visualization, Writing - Original draft. Y. Xu: Conceptualization, Formal analysis, Writing –
Review & Editing. J. Turini: Investigation, Resources, Data curation. O. Collignon: Conceptualization,
Writing – Review & Editing, Supervision, Funding acquisition. D. Crepaldi: Conceptualization, Writing –
Review & Editing, Supervision, Funding acquisition. R. Bottini: Conceptualization, Writing – Review &
Editing, Supervision, Project administration, Funding acquisition.

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481 **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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485 Acknowledgments

The project was partly funded by a PRIN grant (Project number: 2015PCNJ5F_001) from the Italian Ministry of Education, University and Research (MIUR) awarded to Davide Crepaldi in collaboration with Olivier Collignon and by an European Research Council grant (H2020 ERC G.A. n: 804422) awarded to Roberto Bottini.

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494 References

- Allen, R., & Hulme, C. (2006). Speech and language processing mechanisms in verbal serial recall. *Journal of Memory and Language*, 55(1), 64–88. https://doi.org/10.1016/j.jml.2006.02.002
- Barsalou, L. W., Santos, A., Simmons, W. K., & Wilson, C. D. (2008). Language and simulation in
 conceptual processing. Symbols. 1992, 245–283.
- Barsalou, L. W., Simmons, W. K., Barbey, A. K., & Wilson, C. D. (2003). *Grounding conceptual knowledge in modality-specific systems*. http://tics.trends.com
- Belsley, D. A. (1982). Assessing the presence of harmful collinearity and other forms of weak data
 through a test for signal-to-noise. *Journal of Econometrics*, 20(2), 211–253.
 https://doi.org/10.1016/0304-4076(82)90020-3
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the False Discovery Rate: A Practical and Powerful
 Approach to Multiple Testing. In *Source: Journal of the Royal Statistical Society. Series B* (*Methodological*) (Vol. 57, Issue 1).
- Bertero, M., de Mol, C., & Pike, E. R. (1985). Linear inverse problems with discrete data. I. General
 formulation and singular system analysis. *Inverse Problems*, 1(4), 301–330.
 https://doi.org/10.1088/0266-5611/1/4/004
- Bi, Y. (2021). Dual coding of knowledge in the human brain. In *Trends in Cognitive Sciences* (Vol. 25, Issue
 10, pp. 883–895). Elsevier Ltd. https://doi.org/10.1016/j.tics.2021.07.006
- 512 Binder, J. R., Conant, L. L., Humphries, C. J., Fernandino, L., Simons, S. B., Aguilar, M., & Desai, R. H.
 513 (2016). Toward a brain-based componential semantic representation. *Cognitive Neuropsychology*,
 514 33(3–4), 130–174. https://doi.org/10.1080/02643294.2016.1147426
- 515 Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences*,
 516 15(11), 527–536. https://doi.org/10.1016/j.tics.2011.10.001
- Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical
 review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex*, *19*(12), 2767–
 2796. https://doi.org/10.1093/cercor/bhp055
- Binder, J. R., Westbury, C. F., McKiernan, K. A., Possing, E. T., & Medler, D. A. (2005). Distinct brain
 systems for processing concrete and abstract concepts. *Journal of Cognitive Neuroscience*, *17*(6),
 905–917. https://doi.org/10.1162/0898929054021102
- 523 Borghesani, V., & Piazza, M. (2017). The neuro-cognitive representations of symbols: the case of 524 concrete words. *Neuropsychologia*, *105*(October 2016), 4–17.
- 525 https://doi.org/10.1016/j.neuropsychologia.2017.06.026
- Bottini, R., Ferraro, S., Nigri, A., Cuccarini, V., Bruzzone, M. G., & Collignon, O. (2020). Brain Regions
 Involved in Conceptual Retrieval in Sighted and Blind People. *Journal of Cognitive Neuroscience*, 1–
 17. https://doi.org/10.1162/jocn a 01538

Bottini, R., Morucci, P., D'Urso, A., Collignon, O., & Crepaldi, D. (2021). The Concreteness Advantage in
 Lexical Decision Does Not Depend on Perceptual Simulations. *Journal of Experimental Psychology: General*, 151(3), 731–738. https://doi.org/10.1037/xge0001090

- Brown, G. D. A., & Watson, F. L. (1987). First in, first out: Word learning age and spoken word frequency
 as predictors of word familiarity and word naming latency. *Memory & Cognition*, 15(3), 208–216.
 https://doi.org/10.3758/BF03197718
- Carreiras, M., Armstrong, B. C., Perea, M., & Frost, R. (2014). The what, when, where, and how of visual
 word recognition. In *Trends in Cognitive Sciences* (Vol. 18, Issue 2, pp. 90–98).
- 537 https://doi.org/10.1016/j.tics.2013.11.005
- Chen, Y., Davis, M. H., Pulvermüller, F., & Hauk, O. (2013). Task modulation of brain responses in visual
 word recognition as studied using EEG/MEG and fMRI. *Frontiers in Human Neuroscience*, 7(JUN),
 1–14. https://doi.org/10.3389/fnhum.2013.00376
- Chen, Y., Davis, M. H., Pulvermüller, F., & Hauk, O. (2015). Early Visual Word Processing Is Flexible:
 Evidence from Spatiotemporal Brain Dynamics. *Journal of Cognitive Neuroscience*.
- 543 Cohen, L., Lehéricy, S., Chochon, F., Lemer, C., Rivaud, S., & Dehaene, S. (2002). Language-specific tuning
 544 of visual cortex? Functional properties of the Visual Word Form Area. *Brain*, *125*(5), 1054–1069.
 545 https://doi.org/10.1093/brain/awf094
- 546 Connell, L., & Lynott, D. (2012). Strength of perceptual experience predicts word processing
 547 performance better than concreteness or imageability. *Cognition*, *125*(3), 452–465.
 548 https://doi.org/10.1016/j.cognition.2012.07.010
- 549 Crepaldi, D., Amenta, S., Pawel, M., Keuleers, E., & Brysbaert, M. (2015). SUBTLEX-IT. Subtitle-based
 550 word frequency estimates for Italian. *Proceedings of the Annual Meeting of the Italian Association* 551 *For Experimental Psychology*, 10–12.
- Cunningham, J. P., & Yu, B. M. (2014). Dimensionality reduction for large-scale neural recordings. *Nature Neuroscience*, *17*(11), 1500–1509. https://doi.org/10.1038/nn.3776
- Damasio, A. R. (1989). Time-locked multiregional retroactivation: A systems-level proposal for the neural
 substrates of recall and recognition. *Cognition*, *33*(1–2), 25–62. https://doi.org/10.1016/0010 0277(89)90005-X
- Damasio, H., Grabowski, T. J., Tranel, D., Hichwa, R. D., & Damasio, A. R. (1996). A neural basis for lexical
 retrieval Lexical retrieval in subjects with lesions.
- de Groot, A. M. B. (1989). Representational Aspects of Word Imageability and Word Frequency as
 Assessed Through Word Association. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 15*(5), 824–845. https://doi.org/10.1037/0278-7393.15.5.824
- 562 Dhond, R. P., Witzel, T., Dale, A. M., & Halgren, E. (2007). Spatiotemporal cortical dynamics underlying
 563 abstract and concrete word reading. *Human Brain Mapping*, *28*(4), 355–362.
 564 https://doi.org/10.1002/hbm.20282

Dufau, S., Grainger, J., Midgley, K. J., & Holcomb, P. J. (2015). A Thousand Words Are Worth a Picture:
 Snapshots of Printed-Word Processing in an Event-Related Potential Megastudy. *Psychological Science*, *26*(12), 1887–1897. https://doi.org/10.1177/0956797615603934

- Fedorenko, E., Behr, M. K., & Kanwisher, N. (2011). Functional specificity for high-level linguistic
 processing in the human brain. *Proceedings of the National Academy of Sciences of the United*
- 570 States of America, 108(39), 16428–16433. https://doi.org/10.1073/pnas.1112937108
- 571 Fischl, B. (2012). FreeSurfer. *NeuroImage*, *62*(2), 774–781.
- 572 https://doi.org/10.1016/j.neuroimage.2012.01.021

Fliessbach, K., Weis, S., Klaver, P., Elger, C. E., & Weber, B. (2006). The effect of word concreteness on
recognition memory. *NeuroImage*, *32*(3), 1413–1421.
https://doi.org/10.1016/j.neuroimage.2006.06.007

576 Friederici, A. D. (2011). THE BRAIN BASIS OF LANGUAGE PROCESSING: FROM STRUCTURE TO FUNCTION.
 577 *Physiol Rev, 91*, 1357–1392. https://doi.org/10.1152/physrev.00006.2011.-Lan

García, A. M., Moguilner, S., Torquati, K., García-Marco, E., Herrera, E., Muñoz, E., Castillo, E. M.,
Kleineschay, T., Sedeño, L., & Ibáñez, A. (2019). How meaning unfolds in neural time: Embodied
reactivations can precede multimodal semantic effects during language processing. *NeuroImage*, *197*(March), 439–449. https://doi.org/10.1016/j.neuroimage.2019.05.002

Grainger, J., & Holcomb, P. J. (2009). Watching the word go by: On the time-course of component
processes in visual word recognition. *Linguistics and Language Compass*, 3(1), 128–156.
https://doi.org/10.1111/j.1749-818X.2008.00121.x

Groppe, D. M., Urbach, T. P., & Kutas, M. (2011). Mass univariate analysis of event-related brain
potentials/fields I: A critical tutorial review. In *Psychophysiology* (Vol. 48, Issue 12, pp. 1711–1725).
Blackwell Publishing Inc. https://doi.org/10.1111/j.1469-8986.2011.01273.x

Günther, F., Rinaldi, L., & Marelli, M. (2019). Vector-Space Models of Semantic Representation From a
 Cognitive Perspective: A Discussion of Common Misconceptions. *Perspectives on Psychological Science*, 14(6), 1006–1033. https://doi.org/10.1177/1745691619861372

- Halgren, E., Dhond, R. P., Christensen, N., van Petten, C., Marinkovic, K., Lewine, J. D., & Dale, A. M.
 (2002). N400-like magnetoencephalography responses modulated by semantic context, word
- 593 frequency, and lexical class in sentences. *NeuroImage*, *17*(3), 1101–1116.
- 594 https://doi.org/10.1006/nimg.2002.1268
- Hämäläinen, M. S., & Ilmoniemi, R. J. (1994). Interpreting magnetic fields of the brain: minimum norm
 estimates. *Medical & Biological Engineering & Computing*, 32(1), 35–42.
 https://doi.org/10.1007/BF02512476
- Harnad, S. (1990). THE SYMBOL GROUNDING PROBLEM. In *Physica D* (Vol. 42).
- Hauk, O., Davis, M. H., Ford, M., Pulvermüller, F., & Marslen-Wilson, W. D. (2006). The time course of
 visual word recognition as revealed by linear regression analysis of ERP data. *NeuroImage*, *30*(4),
 1383–1400. https://doi.org/10.1016/j.neuroimage.2005.11.048

Hauk, O., Pulvermüller, F., Ford, M., Marslen-Wilson, W. D., & Davis, M. H. (2009). Can I have a quick

- 603 word? Early electrophysiological manifestations of psycholinguistic processes revealed by event-604 related regression analysis of the EEG. *Biological Psychology*, *80*(1), 64–74.
- 605 https://doi.org/10.1016/j.biopsycho.2008.04.015
- Hauk, O., Shtyrov, Y., & Pulvermüller, F. (2008). The time course of action and action-word
- 607 comprehension in the human brain as revealed by neurophysiology. *Journal of Physiology Paris*, 608 102(1–3), 50–58. https://doi.org/10.1016/j.jphysparis.2008.03.013
- Hoffman, P., Binney, R. J., & Lambon Ralph, M. A. (2015). Differing contributions of inferior prefrontal
 and anterior temporal cortex to concrete and abstract conceptual knowledge. *Cortex*, *63*, 250–266.
 https://doi.org/10.1016/j.cortex.2014.09.001
- Hoffman, P., Lambon Ralph, M. A., & Rogers, T. T. (2013). Semantic diversity: A measure of semantic
 ambiguity based on variability in the contextual usage of words. *Behavior Research Methods*, 45(3),
 718–730. https://doi.org/10.3758/s13428-012-0278-x
- Huang, M. X., Mosher, J. C., & Leahy, R. M. (1999). A sensor-weighted overlapping-sphere head model
 and exhaustive head model comparison for MEG. *Physics in Medicine and Biology*, 44(2), 423–440.
 https://doi.org/10.1088/0031-9155/44/2/010
- Hultén, A., van Vliet, M., Kivisaari, S., Lammi, L., Lindh-Knuutila, T., Faisal, A., & Salmelin, R. (2021). The
 neural representation of abstract words may arise through grounding word meaning in language
 itself. *Human Brain Mapping*, 42(15), 4973–4984. https://doi.org/10.1002/hbm.25593
- Jackson, R. L., Hoffman, P., Pobric, G., & Lambon Ralph, M. A. (2016). The semantic network at work and
 rest: Differential connectivity of anterior temporal lobe subregions. *Journal of Neuroscience*, *36*(5),
 1490–1501. https://doi.org/10.1523/JNEUROSCI.2999-15.2016
- Kana, R. K., Blum, E. R., Ladden, S. L., & ver Hoef, L. W. (2012). "How to do things with Words": Role of
 motor cortex in semantic representation of action words. *Neuropsychologia*, *50*(14), 3403–3409.
 https://doi.org/10.1016/j.neuropsychologia.2012.09.006
- 627 Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychtoolbox-3?
- Kroll, J. F., & Merves, J. S. (1986). Lexical Access for Concrete and Abstract Words. In *Journal of Experimental Psychology: Learning, Memory, and Cognition* (Vol. 12, Issue 1).
- Kronbichler, M., Hutzler, F., Wimmer, H., Mair, A., Staffen, W., & Ladurner, G. (2004). The visual word
 form area and the frequency with which words are encountered: Evidence from a parametric fMRI
 study. *NeuroImage*, *21*(3), 946–953. https://doi.org/10.1016/j.neuroimage.2003.10.021
- Lambon-Ralph, M. A., Jefferies, E., Patterson, K., & Rogers, T. T. (2017). The neural and computational
 bases of semantic cognition. *Nature Reviews Neuroscience*, *18*(1), 42–55.
 https://doi.org/10.1038/nrn.2016.150
- Marinkovic, K., Dhond, R. P., Dale, A. M., Glessner, M., Carr, V., & Halgren, E. (2003). Spatiotemporal
 dynamics of modality-specific and supramodal word processing. *Neuron*, *38*(3), 487–497.
 https://doi.org/10.1016/S0896-6273(03)00197-1

639 Miozzo, M., Pulvermüller, F., & Hauk, O. (2015). Early parallel activation of semantics and phonology in

- picture naming: Evidence from a multiple linear regression MEG study. *Cerebral Cortex*, 25(10),
 3343–3355. https://doi.org/10.1093/cercor/bhu137
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for
- advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, 2011. https://doi.org/10.1155/2011/156869
- Paivio, A. (1986). Mental Representations: A dual coding approach. In *Mental Representations: A Dual Coding Approach: Vol.*. Oxford University Press.
- 647 https://doi.org/10.1093/acprof:oso/9780195066661.001.0001
- Paivio, A. (1991). Dual coding theory: Retrospect and current status. *Canadian Journal of Psychology/Revue Canadienne de Psychologie*, 45(3), 255–287. https://doi.org/10.1037/h0084295
- Patterson, K., & Erzinçlioğlu, S. W. (2008). Drawing as a 'window' on deteriorating conceptual knowledge
 in neurodegenerative disease. In *Drawing and the Non-Verbal Mind* (pp. 281–304). Cambridge
 University Press. https://doi.org/10.1017/CBO9780511489730.014
- Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The
 representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, 8(12),
 976–987. https://doi.org/10.1038/nrn2277
- Pulvermüller, F. (2013). How neurons make meaning: Brain mechanisms for embodied and abstractsymbolic semantics. *Trends in Cognitive Sciences*, *17*(9), 458–470.
 https://doi.org/10.1016/j.tics.2013.06.004
- Pulvermüller, F., Shtyrov, Y., & Ilmoniemi, R. (2005). Brain signatures of meaning access in action word
 recognition. *Journal of Cognitive Neuroscience*, *17*(6), 884–892.
- 661 https://doi.org/10.1162/0898929054021111
- Pylkkänen, L., & Marantz, A. (2003). Tracking the time course of word recognition with MEG. *Trends in Cognitive Sciences*, 7(5), 187–189. https://doi.org/10.1016/S1364-6613(03)00092-5
- Rogers, T. T., & Patterson, K. (2007). Object Categorization: Reversals and Explanations of the Basic-Level
 Advantage. *Journal of Experimental Psychology: General*, *136*(3), 451–469.
 https://doi.org/10.1037/0096-3445.136.3.451
- Sabsevitz, D. S., Medler, D. A., Seidenberg, M., & Binder, J. R. (2005). Modulation of the semantic system
 by word imageability. *NeuroImage*, *27*(1), 188–200.
- 669 https://doi.org/10.1016/j.neuroimage.2005.04.012
- Schurz, M., Sturm, D., Richlan, F., Kronbichler, M., Ladurner, G., & Wimmer, H. (2010). A dual-route
 perspective on brain activation in response to visual words: Evidence for a length by lexicality
 interaction in the visual word form area (VWFA). *NeuroImage*, *49*(3), 2649–2661.
 https://doi.org/10.1016/j.neuroimage.2009.10.082
- Schuster, S., Hawelka, S., Hutzler, F., Kronbichler, M., & Richlan, F. (2016). Words in Context: The Effects
 of Length, Frequency, and Predictability on Brain Responses during Natural Reading. *Cerebral Cortex*, 26(10), 3889–3904. https://doi.org/10.1093/cercor/bhw184

677 Schwanenflugel, P. J., Kippharnishfeger, K., Stowe, R., & Hall, A. (1988). Context Availability and Lexical 678 Decisions for Abstract and Concrete Words. In JOURNAL OF MEMORY AND LANGUAGE (Vol. 21). 679 Schwanenflugel, P. J., & Stowe, R. W. (1989). Context Availability and the Processing of Abstract and 680 Concrete Words in Sentences. In Source: Reading Research Quarterly (Vol. 24, Issue 1). Winter. 681 Searle, J. R. (1980). Minds, brains, and programs. Behavioral and Brain Sciences, 3(3), 417–424. 682 https://doi.org/10.1017/S0140525X00005756 683 Smith, E. E., Shoben, E. J., & Rips, L. J. (1974). Structure and process in semantic memory: A featural 684 model for semantic decisions. *Psychological Review*, 81(3), 214–241. 685 https://doi.org/10.1037/h0036351 686 Striem-Amit, E., Wang, X., Bi, Y., & Caramazza, A. (2018). Neural representation of visual concepts in people born blind. Nature Communications, 9(1). https://doi.org/10.1038/s41467-018-07574-3 687 688 Tadel, F., Baillet, S., Mosher, J. C., Pantazis, D., & Leahy, R. M. (2011). Brainstorm: A user-friendly 689 application for MEG/EEG analysis. Computational Intelligence and Neuroscience, 2011. 690 https://doi.org/10.1155/2011/879716 691 van Elk, M., van Schie, H. T., Zwaan, R. A., & Bekkering, H. (2010). The functional role of motor activation 692 in language processing: Motor cortical oscillations support lexical-semantic retrieval. NeuroImage, 693 50(2), 665–677. https://doi.org/10.1016/j.neuroimage.2009.12.123 694 van Heuven, W. J. B., Mandera, P., Keuleers, E., & Brysbaert, M. (2014). SUBTLEX-UK: A new and 695 improved word frequency database for British English. Quarterly Journal of Experimental 696 Psychology, 67(6), 1176–1190. https://doi.org/10.1080/17470218.2013.850521 697 Vigliocco, G., Meteyard, L., Andrews, M., & Kousta, S. (2009). Toward a theory of semantic 698 representation. Language and Cognition, 1(2), 219–247. https://doi.org/10.1515/langcog.2009.011 699 Visser, M., & Lambon Ralph, M. A. (2011). Differential contributions of bilateral ventral anterior 700 temporal lobe and left anterior superior temporal gyrus to semantic processes. Journal of Cognitive 701 Neuroscience, 23(10), 3121–3131. https://doi.org/10.1162/jocn a 00007 702 Wang, J., Conder, J. A., Blitzer, D. N., & Shinkareva, S. v. (2010). Neural representation of abstract and 703 concrete concepts: A meta-analysis of neuroimaging studies. Human Brain Mapping, 31(10), 1459– 704 1468. https://doi.org/10.1002/hbm.20950 705 Wang, X., Men, W., Gao, J., Caramazza, A., & Bi, Y. (2020). Two Forms of Knowledge Representations in 706 the Human Brain. Neuron, 107(2), 383-393.e5. https://doi.org/10.1016/j.neuron.2020.04.010 707 Wilson-Mendenhall, C. D., Simmons, W. K., Martin, A., & Barsalou, L. W. (2013). Contextual processing of 708 abstract concepts reveals neural representations of nonlinguistic semantic content. Journal of 709 Cognitive Neuroscience, 25(6), 920–935. https://doi.org/10.1162/jocn a 00361 710 Xu, Y., He, Y., & Bi, Y. (2017). A tri-network model of human semantic processing. In Frontiers in 711 Psychology (Vol. 8, Issue SEP). Frontiers Media S.A. https://doi.org/10.3389/fpsyg.2017.01538 712