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# **Varieties of semantic cognition revealed through simultaneous decomposition of intrinsic brain connectivity and behaviour**

Deniz Vatansever<sup>1</sup>, Danilo Bzdok<sup>2,3,4</sup>, Hao-Ting Wang<sup>1</sup>, Giovanna Mollo<sup>1</sup>, Mladen Sormaz<sup>1</sup>, Charlotte Murphy<sup>1</sup>, Theodoros Karapanagiotidis<sup>1</sup>, Jonathan Smallwood<sup>1</sup> & Elizabeth Jefferies<sup>1</sup>.

<sup>1</sup> Department of Psychology, University of York, Heslington, York, United Kingdom.

<sup>2</sup> Department of Psychiatry, Psychotherapy and Psychosomatics, Medical Faculty, RWTH Aachen, Germany

<sup>3</sup> JARA, Translational Brain Medicine, Aachen, Germany

<sup>4</sup> Parietal team, INRIA, Neurospin, bat 145, CEA Saclay, 91191 Gif-sur-Yvette, France

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*Address for correspondence:*

Deniz Vatansever, PhD

Post-doctoral Research Associate

Department of Psychology

University of York

Heslington, York, YO10 5DD

Tel: +44 (0) 1904 322889

E-mail: deniz.vatanesever@york.ac.uk

## Abstract

Contemporary theories assume that semantic cognition emerges from a neural architecture in which different component processes are combined to produce aspects of conceptual thought and behaviour. In addition to the state-level, momentary variation in brain connectivity, individuals may also differ in their propensity to generate particular configurations of such components, and these trait-level differences may relate to individual differences in semantic cognition. We tested this view by exploring how variation in intrinsic brain functional connectivity between semantic nodes in fMRI was related to performance on a battery of semantic tasks in 154 healthy participants. Through simultaneous decomposition of brain functional connectivity and semantic task performance, we identified distinct components of semantic cognition at rest. In a subsequent validation step, these data-driven components demonstrated explanatory power for neural responses in an fMRI-based semantic localiser task and variation in self-generated thoughts during the resting-state scan. Our findings showed that good performance on harder semantic tasks was associated with relative segregation at rest between frontal brain regions implicated in controlled semantic retrieval and the default mode network. Poor performance on easier tasks was linked to greater coupling between the same frontal regions and the anterior temporal lobe; a pattern associated with deliberate, verbal thematic thoughts at rest. We also identified components that related to qualities of semantic cognition: relatively good performance on pictorial semantic tasks was associated with greater separation of angular gyrus from frontal control sites and greater integration with posterior cingulate and anterior temporal cortex. In contrast, good speech production was linked to the separation of angular gyrus, posterior cingulate and temporal lobe regions. Together these data show that quantitative and qualitative variation in semantic cognition across individuals emerges from variations in the interaction of nodes within distinct functional brain networks.

## 31 **1. Introduction**

32

33 Semantic cognition allows us to understand the meaning of words, objects,  
34 places and people, and guides our thoughts and actions in a manner that suits  
35 the circumstances (Jefferies, 2013; Lambon Ralph et al., 2016; Patterson et al.,  
36 2007). In addition, this type of cognition also plays a critical role in thoughts that  
37 are unconnected from the here and now, such as when we daydream about a  
38 future achievement or remember a past event (Binder et al., 2009; Smallwood et  
39 al., 2016). Contemporary accounts suggest that semantic cognition emerges from  
40 the interactions of multiple components, supported by distinct brain networks  
41 (Jefferies and Lambon Ralph, 2006; Lambon Ralph et al., 2016). Studies have  
42 recently begun to address how these between-network interactions might  
43 momentarily change, depending on task demands (Bianchi et al., 2013; Davey et  
44 al., 2016; Hallam et al., 2016; Jung and Lambon Ralph, 2016; Krieger-Redwood et  
45 al., 2016). However, relatively little is known about individual differences in  
46 semantic cognition i.e. aspects of brain connectivity that are associated with  
47 trait-level variability in semantic task performance.

48

49 From the component process perspective, semantic cognition is thought to  
50 involve the interaction of semantic representations and control processes that  
51 tailor retrieval to suit the behavioural circumstances (Jefferies, 2013; Lambon  
52 Ralph et al., 2016). Evidence suggests that the semantic representations in long-  
53 term memory draw on modality-specific brain regions (supporting visual and  
54 verbal features, such as our knowledge that zebras have black and white stripes,  
55 and linguistic associations, such as “zebra crossing” (Buccino et al., 2016;  
56 Fernandino et al., 2016)), as well as heteromodal areas, including the anterior  
57 temporal lobe (Lambon Ralph et al., 2016; Patterson et al., 2007). Anterior  
58 temporal cortex is argued to provide a graded “hub” supporting the convergence  
59 of diverse unimodal semantic features. This permits the extraction of deep  
60 conceptual similarity incorporating both verbal and non-verbal knowledge. In  
61 addition, since we all know a diverse range of features and associations to any  
62 given concept, conceptual retrieval must be constrained in accordance with goals  
63 and environmental conditions (Badre et al., 2005; Jefferies and Lambon Ralph,

64 2006; Thompson-Schill et al., 1997). Hence, semantic control processes may play  
65 a vital role in focusing retrieval on currently relevant aspects of knowledge and  
66 supressing strongly encoded but currently irrelevant information. This aspect of  
67 semantic cognition is thought to be supported by a distinct set of brain regions  
68 including domain-general executive areas (e.g. dorsal/posterior inferior frontal  
69 gyrus, pre-supplementary motor area) and areas more specifically implicated in  
70 semantic control (e.g. ventral/anterior inferior frontal gyrus, posterior middle  
71 temporal gyrus (Davey et al., 2016; Noonan et al., 2013)).

72

73 In line with this interactive view, cognitive neuroscience research has provided  
74 converging evidence for multiple, interrelated components within semantic  
75 cognition. Lesion studies have revealed that selective damage to the anterior  
76 temporal lobe, left inferior frontal gyrus and/or posterior middle temporal gyrus  
77 produce dissociable impairments, compromising the integrity of conceptual  
78 representations (Bozeat et al., 2000; Patterson et al., 2007), or their use in a goal-  
79 oriented manner, respectively (Jefferies and Lambon Ralph, 2006; Jefferies et al.,  
80 2008; Noonan et al., 2010; Rogers et al., 2015). The functional dissociation  
81 between these brain regions is also supported by neuroimaging (Hoffman et al.,  
82 2015; Humphreys et al., 2015; Noonan et al., 2013) and neurostimulation  
83 (Binney et al., 2010; Davey et al., 2015; Pobric et al., 2007; Whitney et al., 2011)  
84 investigations of semantic processing in healthy participants.

85

86 Recent studies have also shown that although these brain regions act in concert  
87 to support semantic cognition (i.e., they co-activate during task fMRI), they form  
88 distinct large-scale brain networks at rest (Davey et al., 2016; Jackson et al.,  
89 2016), depicting functional integration when participants shift from rest to  
90 semantic tasks (Krieger-Redwood et al., 2016). For example, as an important hub  
91 of semantic processing (Patterson et al., 2007), anterior temporal lobe (ATL)  
92 shows strong connectivity at rest to regions of the default mode network (DMN),  
93 including angular gyrus and posterior cingulate cortex (Jackson et al., 2016;  
94 Murphy et al., 2017). In contrast, semantic control regions such as left inferior  
95 frontal gyrus and posterior middle temporal gyrus show strong intrinsic  
96 connectivity to each other, and they connect to both default mode and fronto-

97 parietal networks (Davey et al., 2016). Together these studies suggest that  
98 semantic cognition is an emergent property of variable interactions between not  
99 only particular brain regions, but also distributed large-scale brain networks,  
100 present at rest and in cognitive tasks (Cole et al., 2014).

101

102 Although this assumption is broadly accepted, it remains unclear how individual  
103 differences in the strength of specific connections within and between these  
104 networks might relate to trait-level differences in semantic abilities. For  
105 example, the strength of particular network interactions might give rise to global  
106 differences in the efficiency of semantic retrieval across tasks, linked to the  
107 tendency to stay on task. Studies have associated both task-based semantic  
108 behaviour and off-task mind-wandering to overlapping brain regions involved in  
109 semantic processing that are allied to the DMN (Binder et al., 2009; Smallwood et  
110 al., 2016). The strength of intrinsic connectivity between these default mode  
111 regions and areas linked to task engagement might therefore determine whether  
112 individuals are generally willing or able to focus semantic retrieval on an  
113 externally-imposed goal, as opposed to conceptual associations that might have  
114 greater personal relevance. In addition, since research has revealed network  
115 differences that relate to the modality of information being retrieved (i.e., words  
116 vs. pictures) and the extent to which semantic control processes are required to  
117 shape retrieval to suit the task, we might expect individual differences in  
118 patterns of intrinsic network connectivity to relate to relative strengths and  
119 weaknesses in these varieties of semantic cognition across participants.

120

121 To assess these hypotheses, we recorded task-based and resting state functional  
122 magnetic resonance imaging (fMRI) data in a large cohort of participants, who  
123 also described their thoughts while at rest inside the scanner. On a subsequent  
124 day, these participants performed a battery of semantic tasks, including  
125 relatedness, identity and feature judgements, picture naming and verbal fluency.  
126 The tasks used different types of stimuli including words and pictures,  
127 manipulated the requirement for controlled retrieval using strong and weak  
128 associations (Badre et al., 2005; Davey et al., 2016), and assessed both  
129 comprehension and production, allowing us to characterise diverse aspects of

130 semantic cognition. We used advanced multivariate statistics (Smith et al., 2015;  
131 Tsvetanov et al., 2016) to simultaneously decompose individual variation in  
132 brain data (resting state connectivity) and behaviour (measured outside the  
133 scanner) to identify the neurocognitive components of semantic cognition. We  
134 confirmed the validity of these components by examining their association with  
135 independent measures: the neural response to meaningful over meaningless  
136 information in task-based fMRI and subjective descriptions of self-generated  
137 thoughts during the resting-state scan (Gorgolewski et al., 2014). This allowed us  
138 to specify neurocognitive components that relate to the (i) average performance  
139 on semantic tasks and (ii) varieties of semantic cognition. Overall, these results  
140 help to elucidate the fundamental mechanisms underpinning variation in  
141 semantic cognition in healthy individuals.

142

143

144 **2. Methods**

145

146 **2.1 Participant Demographics**

147 Ethical approval was obtained from the Department of Psychology and York  
148 Neuroimaging Centre, University of York ethics committees. A total of 165 right-  
149 handed, native English speaker, undergraduate or postgraduate students with  
150 normal to corrected vision were recruited for this study. Informed consent was  
151 sought prior to taking part in the fMRI as well as the behavioural assessments.  
152 The participants received either a monetary reward of £80 or eight hours of  
153 course credit.

154

155 As per the exclusion criteria, none of the participants had a history of psychiatric  
156 or neurological illness, severe claustrophobia, anticipated pregnancy or drug use  
157 that could alter cognitive functioning. In total, 11 participants were excluded  
158 from the analysis; eight due to incomplete behavioural assessment and three  
159 because of registration problems associated with the neuroimaging data.  
160 Consequently, the final group included 154 participants, who completed all the  
161 neuroimaging and behavioural assessments. The average age for this group was  
162 20.20 years (range = 18-31, SD = 2.43) with 94 females.

163

164 **2.2. Behavioural Assessment**

165 Following the imaging protocol, participants took part in a comprehensive set of  
166 behavioural assessments that captured different aspects of semantic cognition.  
167 The tasks were completed over three 2-hour long sessions on different days,  
168 with the order of the sessions counterbalanced across participants. Full details  
169 about the semantic tasks are provided in the supplementary materials (Table S1-  
170 5). In total, there were 12 tasks that examined semantic cognition:

- 171
- 172 • Two 3-alternative forced choice (3AFC) tasks required participants to  
173 identify pictures at two levels of specificity. Superordinate word-picture  
174 matching required participants to link a picture of a Dalmatian with the  
175 word “animal” (as opposed to distractors such as “vehicle; clothes”).  
176 Specific-level matching, however, involved the same probe image and  
specific-level names (e.g., target word “Dalmatian” with distractors



177 “Labrador; Corgi”). Previous research has shown that ventral and medial  
178 aspects of anterior temporal lobe show a stronger response to specific  
179 concepts (Rogers et al., 2006), while greater integration of visual  
180 information in this condition allows similar concepts to be successfully  
181 distinguished (Clarke et al., 2013). In addition, inhibitory transcranial  
182 magnetic stimulation (TMS) to angular gyrus has been shown to disrupt  
183 the retrieval of specific conceptual information using this task (Davey et  
184 al., 2015).

185 • Two 3AFC tasks examined the effect of presentation format, contrasting  
186 verbal semantic judgements (when the probe and response options were  
187 presented as written words) with picture semantic judgements (when  
188 items were presented as pictures). Comparisons of verbal and non-verbal  
189 semantic decisions have been used to distinguish cognitive components  
190 that support amodal and abstract aspects of conceptual processing (such  
191 as ventral anterior temporal lobe), from ‘embodied’ or modality-specific  
192 aspects (Bright et al., 2004; Patterson et al., 2007; Vandenberghe et al.,  
193 1996; Visser et al., 2012).

194 • Two 3AFC tasks assessed the retrieval of strong and weak semantic  
195 associations. These judgements presented a picture probe and three  
196 response options as words (in line with the identity-matching tasks). The  
197 strength of association between the probe and target was manipulated.  
198 Previous studies focusing on the neural basis of controlled semantic  
199 retrieval have frequently used contrasts of strong versus weak  
200 associations, and have commonly reported greater activation within left  
201 inferior frontal gyrus and posterior middle temporal gyrus when the  
202 relevant link is harder to retrieve (Badre et al., 2005; Davey et al., 2016;  
203 Gold and Buckner, 2002; Krieger-Redwood et al., 2015).

204 • A feature-matching task (presented in the form of 3AFC) assessed the  
205 ability to match probe and target words based on a specific semantic  
206 feature (e.g., colour, shape, size, texture). One of the distractors was a  
207 strong global associate that had to be ignored. This task is thought to  
208 require goal-driven selection of relevant knowledge (Badre et al., 2005)  
209 and has been shown to strongly activate dorsal aspects of the left inferior

210 frontal gyrus and other regions within the multiple-demand system  
211 (Davey et al., 2016; Duncan, 2010). Thus, we included tasks that tapped  
212 two potentially separable aspects of semantic control: top-down feature  
213 selection (in the feature matching task) and recovery of weakly-encoded  
214 associations in a more bottom-up fashion (Badre et al., 2005; Davey et al.,  
215 2016).

- 216 • A 3AFC task that required pattern matching of meaningless scrambled  
217 images was employed as a control task. It had similar decision-making  
218 and response requirements as the semantic tasks described above.
- 219 • Picture naming task required participants to say aloud the most specific  
220 name possible for a set of common objects.
- 221 • Three verbal fluency tasks required participants to list as many items as  
222 possible within one minute. There were four general categories (e.g.  
223 animals, fruit, vehicles, tools), two specific categories (e.g. types of birds  
224 and types of boat) and three letters (e.g. F,A,S).

225

### 226 **2.3 Neuroimaging Data Acquisition**

227 The scanning session was carried out at the York Neuroimaging Centre, York  
228 with a 3T GE HDx Excite Magnetic Resonance Imaging (MRI) scanner using an  
229 eight-channel phased array head coil. Following a T1-weighted structural scan  
230 with 3D fast spoiled gradient echo (TR = 7.8 s, TE = minimum full, flip angle= 20°,  
231 matrix size = 256 x 256, 176 slices, voxel size = 1.13 x 1.13 x 1 mm) and a FLAIR  
232 sequence, a nine-minute resting state fMRI scan was carried out using single-  
233 shot 2D gradient-echo-planar imaging (TR = 3 s, TE = minimum full, flip angle =  
234 90°, matrix size = 64 x 64, 60 slices, voxel size = 3 x 3 x 3 mm<sup>3</sup>, 180 volumes).  
235 During resting state scanning, the participants were asked to focus on a fixation  
236 cross and not to think of anything in particular.

237

238 Using the same scanning parameters as for the resting state scans, we also  
239 acquired a semantic localiser task in which the participants were asked to  
240 passively view meaningful (e.g., her + secrets + were + written + in + her + diary)  
241 and meaningless sequences of non-words (e.g. crark + dof + toin + mesk + int +  
242 lisal + glod + flid). A total of 10 sentences with meaningful content, based on

243 Rodd et al. (2005), and 10 meaningless sentences with nonsensical content,  
244 matched in word length and number of syllables, were presented in two blocks  
245 of five (i.e., a total of 4-blocks), in a pseudo-random order. While transition  
246 between blocks was denoted by a task instruction (e.g., Meaningful), a red  
247 fixation marked the end of each sentence, with a jittered duration of 4000-  
248 6000ms. Each sentence was presented one word at a time (600 ms) to ensure  
249 that the speed of reading was matched across meaningful and non-meaningful  
250 stimuli, interleaved by 250 ms fixation periods.

251

## 252 **2.4 Neuroimaging Data Pre-processing**

253 All functional data were pre-processed using a standard pipeline, and analysed  
254 via FMRIB Software Library (FSL Version 6.0). The spatial pre-processing of the  
255 resting state functional data involved motion correction via MCFLIRT, slice-  
256 timing correction with Fourier space time-series phase-shifting, and  
257 normalisation to the MNI-152 template space using FLIRT as well as skull-  
258 stripped FLAIR and T1-weighted structural images. In addition, high-pass (sigma  
259 = 200 s) and low-pass temporal filtering (sigma = 2.8 s) was applied in order to  
260 focus on the slow-wave fluctuations. Finally, the confounding six motion  
261 parameters as well as the top 5 PCA components of the cerebrospinal fluid and  
262 white matter signal was removed using the CompCor method (Behzadi et al.,  
263 2007). This eliminated the need for a global signal regression that is reported to  
264 introduce spurious anti-correlations (Chai et al., 2012; Murphy et al., 2009). No  
265 spatial smoothing was applied. The same pre-processing pipeline was also  
266 applied to the semantic localiser functional neuroimaging data, except for the  
267 low-pass temporal filtering.

268

## 269 **2.5 ROI Definitions and Functional Connectivity Matrix Construction**

270 In order to objectively identify a set of semantic regions of interest (ROIs) that  
271 formed the brain functional connectivity matrices, we selected spatial maps from  
272 the literature that covered large-scale brain networks previously implicated in  
273 semantic cognition (Fig. 1A). We started with a meta-analytic map of “semantic”  
274 processing derived from Neurosynth, and identified regions on this map that fell  
275 within two distinct networks: the default mode network (DMN – associated with

276 relatively easy semantic judgements and the presentation of strongly coherent  
277 conceptual combinations (Bemis and Pylkkanen, 2013; Davey et al., 2016;  
278 Humphreys et al., 2015; Price et al., 2016)) and the semantic control network  
279 (associated with harder semantic judgements and the presentation of weak  
280 conceptual combinations (Noonan et al., 2013)). The DMN was selected from the  
281 Yeo7 parcellation of whole-brain functional connectivity (Yeo et al., 2011) and  
282 downloaded from the Freesurfer website ([https://surfer.nmr.mgh.harvard.edu](https://surfer.nmr.mgh.harvard.edu/fswiki/CorticalParcellation_Yeo2011)  
283 /fswiki/CorticalParcellation\_Yeo2011), while the semantic control map was  
284 taken from the Noonan et al. (2013) meta-analysis of 53 semantic cognition  
285 studies that varied the required level of executive control. The binarised maps of  
286 these two contrasting networks were overlaid on the false-positive discovery  
287 rate corrected, statistical co-activation map ( $P_{\text{term}} | \text{activation}$ ) of the “semantic”  
288 term in the Neurosynth database (accessed May 2016), and masked with the  
289 Automated Anatomical Labelling (AAL) map.

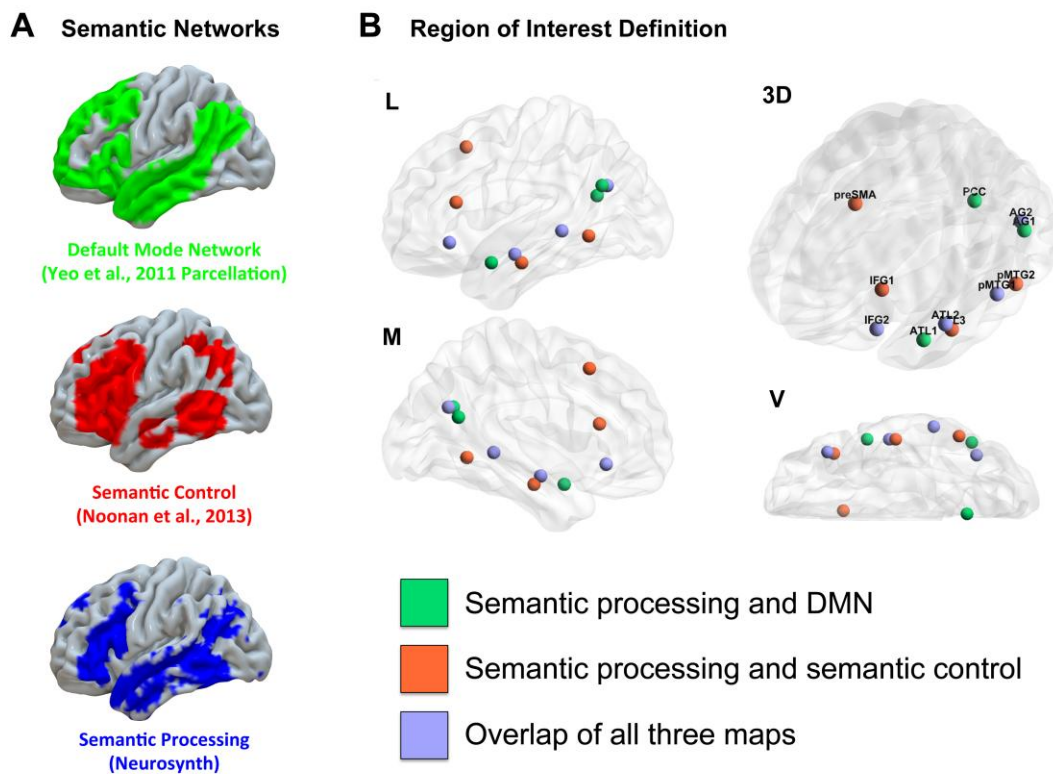
290

291 Using this procedure, we identified clusters of voxels where the Neurosynth  
292 semantic map overlapped with the DMN in anterior temporal lobe, ventral  
293 angular gyrus and posterior cingulate cortex. Moreover, the Neurosynth  
294 semantic map was overlapped with regions implicated in semantic control in  
295 posterior inferior frontal gyrus, pre-supplementary motor area, posterior middle  
296 temporal gyrus and ventral-mid-middle temporal gyrus. Finally, we identified  
297 regions where the Neurosynth semantic map overlapped with *both* the default  
298 mode and the semantic control networks, in anterior inferior frontal gyrus,  
299 posterior middle temporal gyrus, middle temporal gyrus and dorsal angular  
300 gyrus. Brain regions in the right hemisphere were omitted to improve the  
301 interpretability of the results and to solve the limitations associated with the CCA  
302 technique. The resulting 11 regions were used to extract BOLD signal time-series  
303 based on 6 mm seed spheres placed in the centre of these regions (Fig. 1B). Z-  
304 scored Pearson correlation coefficients of the signal between each of the 11 ROIs  
305 defined the functional connectivity matrices for each participant, utilised in the  
306 subsequent brain and behaviour decomposition analysis.

307

308 **2.6 Sparse Canonical Correlation Analysis**

309 With the aim of collectively characterising patterns of brain connectivity and  
 310 behavioural performance measured outside the scanner, we employed a  
 311 multivariate pattern analysis technique, canonical correlation analysis (CCA).  
 312 Over and above independent components analysis of neuroimaging data  
 313 (Beckmann et al., 2005), CCA identifies distinct canonical components from the  
 314 linear combinations of two variable spaces (behaviour and brain). Thus, this  
 315 technique allowed us to test the component process hypothesis by describing the  
 316 relationship between intrinsic brain functional connectivity and semantic task  
 317 performance simultaneously (Hardoon et al., 2004).  
 318



319 **Figure 1 Definition of semantic ROIs. A)** The seeds used for the simultaneous decomposition analysis  
 320 were objectively defined as overlaps between the meta-analytic map derived for the term “semantic” from  
 321 the Neurosynth database, and two large-scale brain networks previously implicated in semantic cognition: a  
 322 semantic control network based on Noonan et al.’s (2013) meta-analysis of fMRI studies, plus the DMN as  
 323 defined by Yeo et al.’s (2011) 7-network parcellation of whole-brain functional connectivity. ROIs were  
 324 defined as being within the Neurosynth map (i.e., relevant for semantic cognition) and (i) also in the DMN;  
 325 (ii) also in the semantic control map; (iii) also in both DMN and the semantic control maps. The resulting  
 326 regions were masked with the AAL atlas for labelling purposes and 6 mm seeds were placed in the centre of  
 327 each area of overlap, creating seed regions for the functional connectivity analysis. **B)** A total of 11 semantic  
 328 ROIs were included in this analysis (visualised on an MNI152 glass brain). The posterior cingulate cortex  
 329

330 (PCC), angular gyri (AG1) and temporal pole (ATL1) fell within the DMN (green). The semantic control  
331 network included regions in the pre-supplementary motor area (pre-SMA), posterior middle temporal  
332 gyrus (posterior pMTG2), posterior inferior frontal gyrus (pIFG1) as well as mid-MTG (ATL3; orange). A few  
333 regions were common to both the default mode and the semantic control networks (anterior IFG2; anterior  
334 pMTG1; ATL2, light blue).

335 The standardized (unit variance scaled and mean-centred) functional  
336 connectivity matrices as well as the standardized behavioural scores were fed  
337 into a reliable and robust implementation of the CCA method, using the  
338 Penalised Multivariate Analysis (PMA) R package from the CRAN repository. In  
339 order to improve the interpretability of the obtained decomposition solutions  
340 (Hastie et al., 2015), we applied an  $L_1$ -penalised variant of CCA introduced by  
341 Witten et al. (2009). This is achieved by setting a maximum number of brain or  
342 behaviour variables to exactly zero, which in turn cancels their contribution to  
343 the prediction goal and increases the sparseness of the solutions. This results in  
344 a regularised version of the singular value decomposition, reducing the excess  
345 information to meaningful decompositions. In other words, this sparsity  
346 (variable selection) method considers the entire model to derive canonical  
347 components, automatically de-weighting variables as unimportant if they did not  
348 explain variation in the data. In the current analysis, the  $L_1$  penalty on resting  
349 state functional connectivity was 0.4, and 0.5 on the behavioural performance.  
350 The resulting brain and behaviour components were visualised using BrainNet  
351 Viewer on a glass MNI152 brain, in three different planes (Xia et al., 2013). In  
352 addition, circular representations were provided for better visual description of  
353 the components (Irimia et al., 2012) as implemented in Gephi (Version 0.91)  
354 (Bastian et al., 2009).

355

## 356 **2.7 Neurocognitive Pattern Description**

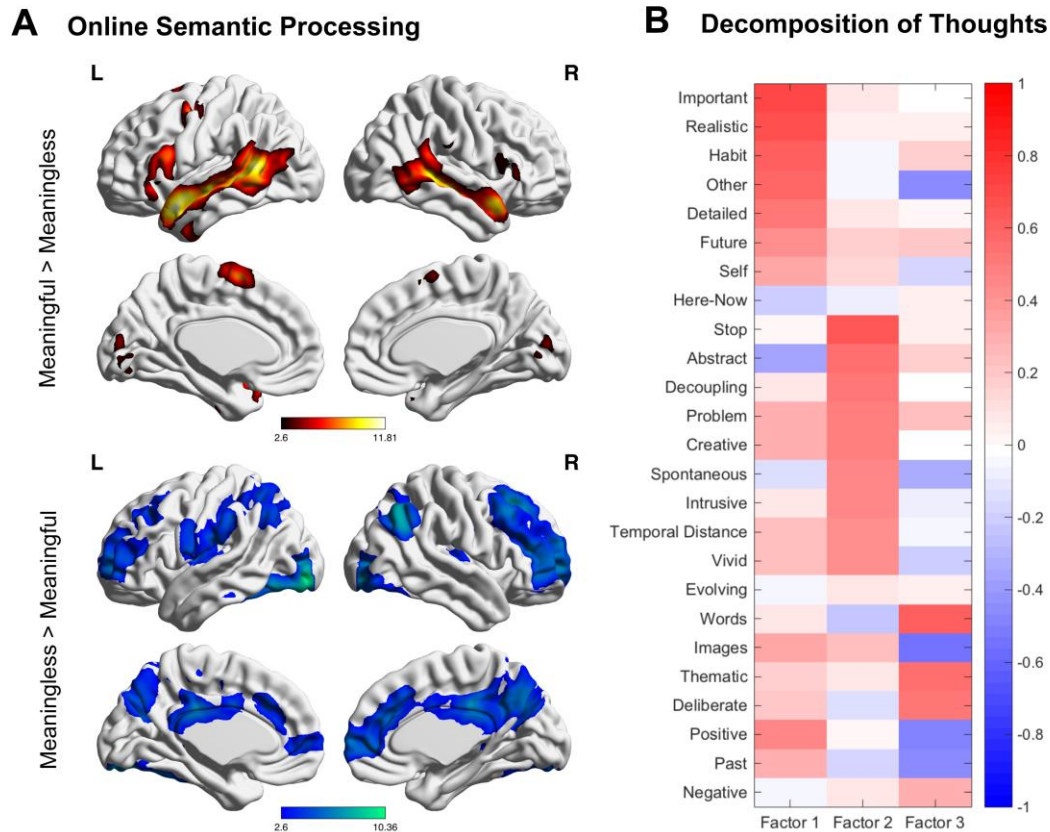
357 Similar to other commonly used decomposition techniques in neuroimaging (e.g.  
358 ICA or PCA), biologically meaningful number of CCA components is determined  
359 by external knowledge. In other words, the number of viable components are  
360 usually determined by the level at which the components identified from one set  
361 of data are still meaningful in a different set of data. This procedure then  
362 validates the interpretability and importance of the identified components. Thus,  
363 our aim was to describe the patterns of brain and behaviour relationships (i.e.

364 varieties of semantic cognition) that were identified from the CCA analysis,  
365 utilising separate datasets. For that purpose, we employed the semantic localiser  
366 task performed inside the scanner, as well as self-report measures of mind-  
367 wandering at the end of the resting state scan.

368

369 For assessing differential BOLD activity in the semantic localiser task, we first  
370 examined the contrast of *meaningful* > *meaningless* task blocks, and the reverse  
371 effect, and confirmed that the task activated brain regions that are expected to be  
372 involved in semantic processing (Fig. 2A). Subsequently, the participant-specific  
373 component expression (i.e. brain and behaviour component loadings from the  
374 CCA for each participant) were carried forward as covariates to the higher-level  
375 activation analysis, collectively forming a group-wise general linear model. We  
376 searched for shared associations between both the brain and the behaviour  
377 component loadings for a given CCA component and beta values from the chosen  
378 task contrast. The resulting clusters were multiple comparison corrected via  
379 Family-Wise Error (FWE) detection technique at a Z threshold greater than 2.6  
380 ( $p < 0.05$ ). The unthresholded statistical maps were uploaded to the NeuroVault  
381 repository (<http://neurovault.org/collections/2108/>). The regions showing a  
382 significant linear relationship between the beta values of the *meaningful* >  
383 *meaningless* contrast and the participants' CCA loadings were visualised on an  
384 MNI152 glass brain. Finally, a conjunction using the minimum statistics method  
385 (Nichols et al., 2005) was used to identify brain regions that showed a  
386 correlation with BOLD activity across all of the relevant CCA components. We  
387 then explored the seed-based functional connectivity of this conjunction region  
388 on an independent dataset, based on the intrinsic functional connectivity  
389 calculations of 1,000 subjects, publicly available on the Neurosynth website (Yeo  
390 et al., 2011). In order to provide an objective description of the multiple roles  
391 that are associated with this conjunction region, we later used the Neurosynth  
392 database (accessed May 2016) to examine the typically associated terms.

393



394  
395

396 **Figure 2 Description of neurocognitive components.** **A)** The CCA components were first validated using  
 397 neuroimaging data acquired during a semantic localiser task. In this paradigm, the participants were  
 398 presented with sequences of words in sequences and non-words, interleaved with a baseline fixation  
 399 condition. The group-level forward and reverse contrasts were cluster corrected at a threshold of  $Z > 2.6$  ( $p$   
 400  $< 0.05$ ). **B)** The components were also validated using the subjective description of the participants'  
 401 thoughts acquired at the end of the resting state scan, using a set of questions that were previously used to  
 402 assess the ongoing mental experiences of participants (Smallwood et al., 2016). The principle components  
 403 covering three main categories of thought – broadly corresponding to realistic, important mental time  
 404 travel, intrusive thought and verbal thematic thoughts are visualised in a heat map displaying Varimax-  
 405 rotated component loadings.

406 Moreover, with the aim of capturing different features of the participants'  
 407 spontaneous mental experiences, we employed a 4-choice questionnaire at the  
 408 end of the resting-state scanning session that required the participants to  
 409 subjectively rate their thoughts from “Not at all” to “Completely” based on a  
 410 series of mind-wandering questions previously used in the literature  
 411 (Gorgolewski et al., 2014; Medea et al., 2016; Ruby et al., 2013a; Ruby et al.,  
 412 2013b; Smallwood et al., 2016). The set of questions are provided in the  
 413 supplementary material (Table S6). Subsequently, the ratings for each



414 participant were reduced to three factors using principal component analysis  
415 (PCA) in SPSS (Version 23), which broadly corresponded to realistic and  
416 important mental time-travel, intrusive thought, and verbal thematic thought.  
417 The component loadings were rotated using the Varimax method and the  
418 resulting factors were visualised on a heat map (Fig. 2B). Using linear  
419 regressions at  $p = 0.05$  level of significance, these mind-wandering components  
420 were related to the average brain and behaviour component loadings obtained  
421 from the CCA analysis.

422

### 423 **3. Results**

424 The main objective of this study was to identify neurocognitive components of  
425 brain and behaviour relationships that described individual differences in  
426 semantic cognition. For that purpose, we first fed in to CCA the standardized  
427 (unit variance scaled and mean-centred) functional connectivity values between  
428 semantic regions at rest and standardized performance values in a battery of  
429 semantic tasks. The identified components were then validated through linear  
430 regressions in separate datasets, originating from the participants' performance  
431 of a semantic localiser fMRI task inside the scanner and their mind-wandering  
432 tendencies captured at the end of the resting state scan. Such a multi-variate,  
433 multi-dataset approach enabled us to objectively assess the relationship between  
434 individual differences in brain connectivity and behaviour, in line with the  
435 component process view of semantic cognition.

436

437 First, Table 1 outlines the mean performance of the participants across all the  
438 behavioural tasks used in the semantic battery. In order to ensure that the  
439 manipulations of semantic strength, semantic category and modality of  
440 presentation produced the expected results previously reported in the literature,  
441 we compared the mean efficiency score (reaction time weighted by accuracy) for  
442 the relatedness and identity-matching tasks with repeated measures paired t-  
443 tests. On average, participants were faster in responding to pictures than words  
444 ( $t(153) = 16.282, p < 0.001$ ), to specific (e.g. Dalmatian) than general (e.g.  
445 animal) terms ( $t(153) = 3.072, p = 0.003$ ), and to strong than weak associations  
446 ( $t(153) = 24.675, p < 0.001$ ).

447

448 Using CCA, of the six neurocognitive components identified, four predicted either  
449 the neural activation recorded during the presentation of meaningful versus  
450 meaningless sentences in task-based fMRI, or the spontaneous thoughts  
451 reported at the end of the resting-state scan. Our findings broadly support the  
452 component process hypothesis, by showing that varieties of semantic cognition  
453 can be related to different strengths of coupling between brain regions at rest.  
454 However, the analysis does not permit us to determine the potential number of  
455 separable components. Thus, in this report we focus on the four components for

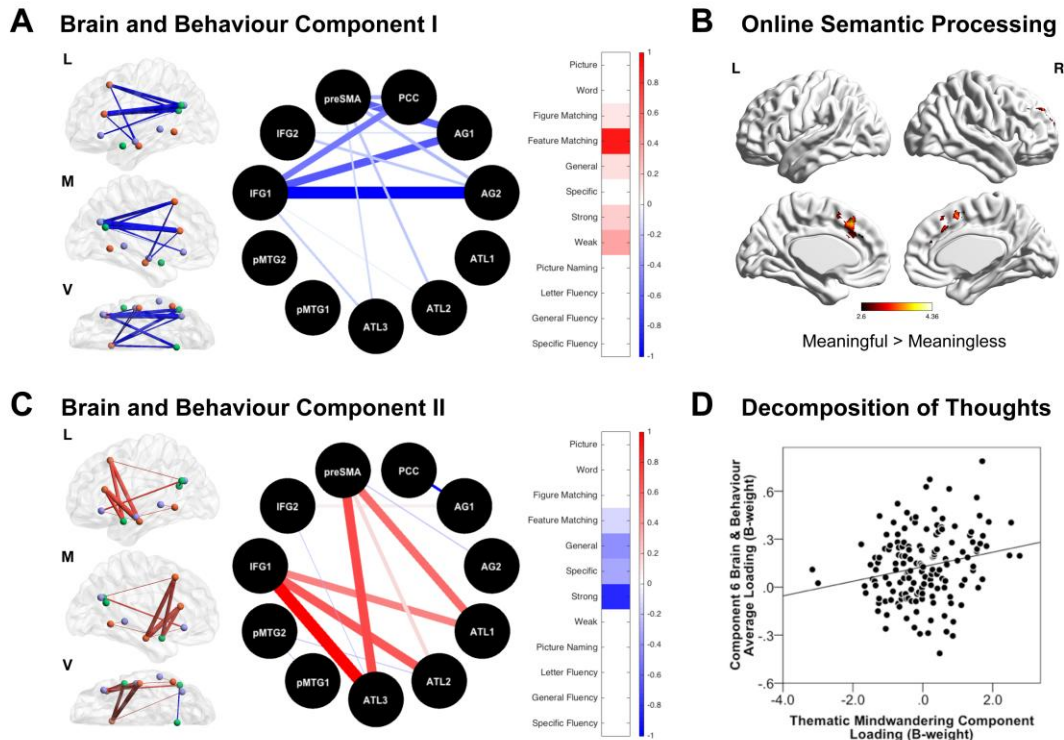
456 which construct validity was demonstrated through a relationship with other  
 457 measures relevant to semantic cognition. The canonical correlations and the  
 458 squared canonical correlated for these four components were 0.25 ( $p = 0.002$ ),  
 459 0.20 ( $p = 0.012$ ), 0.08 ( $p = 0.322$ ), 0.19 ( $p = 0.016$ ) and 0.06, 0.04, 0.01, 0.04,  
 460 respectively. The remaining two components are presented in the  
 461 supplementary materials (Fig. S1).

462

463 **Table 1 Descriptive statistics for the battery of semantic tasks.** For the relatedness, figure matching and  
 464 feature matching tasks, the efficiency score reflected the reaction time divided by the proportion of correct  
 465 responses. For the picture naming task response accuracy was used as the performance measure, whereas  
 466 for the verbal fluency tasks the correct responses per minute were recorded.

<i>SEMANTIC TASK</i>	<i>Minimum</i>	<i>Maximum</i>	<i>Mean</i>	<i>Standard Deviation</i>
<i>Relatedness Task: Picture (Efficiency)</i>	467.55	3267.08	1335.87	345.73
<i>Relatedness Task: Word (Efficiency)</i>	1140.00	2833.33	1775.21	339.50
<i>Non-semantic Figure Matching Task (Efficiency)</i>	1222.64	4345.00	1957.59	489.16
<i>Semantic Feature Matching Task (Efficiency)</i>	1490.53	25740.00	2992.52	2817.89
<i>Word-picture matching: General (Efficiency)</i>	797.29	2661.07	1235.32	241.136
<i>Word-picture matching: Specific (Efficiency)</i>	769.47	2222.99	1200.05	241.065
<i>Relatedness Task: Strong (Efficiency)</i>	947.80	3125.45	1406.50	259.32
<i>Relatedness Task: Weak (Efficiency)</i>	1477.09	6654.07	2419.06	675.71
<i>Picture Naming Task (Accuracy)</i>	0.00	1.00	0.84	0.184
<i>Verbal Fluency Task: Letter (Correct per minute)</i>	6.00	25.30	14.44	3.74
<i>Verbal Fluency Task: Category-General (Correct per minute)</i>	10.00	30.00	18.94	3.70
<i>Verbal Fluency Task: Category-Specific (Correct per minute)</i>	6.75	19.50	12.59	2.60

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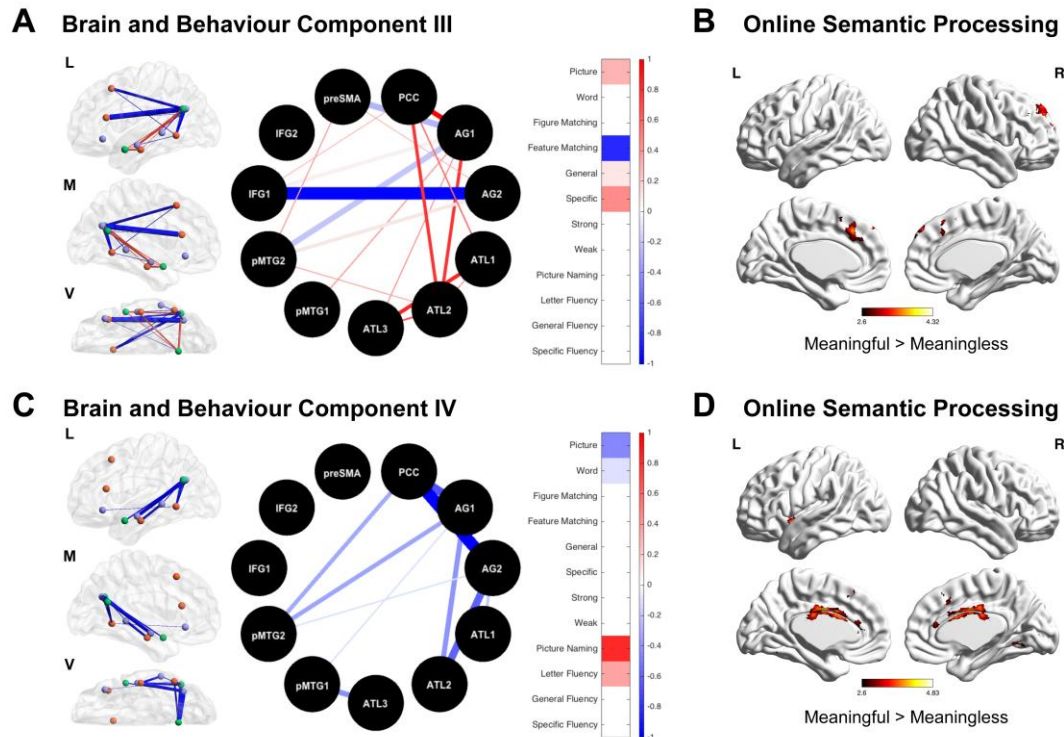
**Figure 3 Neurocognitive components related to global performance in semantic cognition.** The brain connectivity patterns based on the identified canonical components are displayed on an MNI152 glass brain in three different planes: lateral (L), medial (M) and ventral (V), as well as in a circular representation. In both displays, the thickness of the connections between the seed ROIs corresponds to the relative component weights of the functional connections as deviation away from the mean, whereas the colours represent directionality (red-positive, blue-negative). The associated behavioural performance is illustrated on a heatmap. The scale refers to the relative component weights of both the standardized brain functional connections and the standardized behavioural scores. The higher the value (more red), the greater the connectivity and the behavioural performance were. **A)** The first component was characterised by reduced connectivity between the default mode and executive control regions, and was associated with better performance on difficult comprehension tasks (feature matching and weak associations). **B)** Participants that displayed greater component loading on this pattern of brain and behaviour association at rest showed greater activity in the meaningful vs. meaningless contrast of the semantic localiser task, centred on the pre-supplementary motor area (one of the regions that showed decoupling from the default mode at rest). The reported regions were cluster-corrected at a threshold of  $Z > 2.6$  ( $p < 0.05$ ). **C)** Component II described a pattern of strong connectivity between executive control regions (pre-supplementary motor area, inferior frontal gyrus) and the anterior temporal lobe, related to poorer performance, primarily on easier semantic tasks (strong associations and identity matching). **D)** Though this brain and behaviour pattern was not associated with activity in the semantic localiser tasks, it was linked to greater verbal, thematic, and deliberate thoughts reported at the end of the resting state scanning session ( $R = 0.213$ ,  $p = 0.008$ ).

491 The first two brain and behaviour patterns identified using CCA described  
492 general differences in semantic performance measured outside the scanner.  
493 Component I was characterized by patterns of reduced connectivity at rest for  
494 angular gyrus, posterior cingulate and anterior temporal lobe (i.e. default mode  
495 regions) with frontal areas that are linked to executive control (i.e. inferior  
496 frontal gyrus and pre-supplementary area) (Fig. 3A). Participants who strongly  
497 showed this pattern of reduced connectivity at rest showed better performance  
498 on a range of semantic tasks, particularly harder comprehension tasks thought to  
499 depend on semantic control (e.g. matching items based on specific features and  
500 ignoring global associations; identifying weak semantic associations). They also  
501 showed a stronger response in task-based fMRI for the *meaningful > meaningless*  
502 contrast within regions of the cingulate cortex and the pre-supplementary motor  
503 area (Fig. 3B). Thus, they showed separation at rest of one region (pre-  
504 supplementary motor area) that was recruited more strongly by semantic  
505 processing. There was no significant association between this CCA and any  
506 pattern of thoughts reported at rest.

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508 Component II reflected a pattern of stronger coupling of the anterior temporal  
509 lobe with the left inferior frontal gyrus and the pre-supplementary motor area at  
510 rest (Fig. 3C). In terms of behaviour, this component was characterised by poor  
511 performance on tasks that are generally easy to perform, such as relatedness  
512 judgements for strongly associated words, and identity matching. This  
513 component did not vary with neural recruitment in task-based fMRI; however,  
514 regression of the average brain and behaviour component loadings against the  
515 thoughts reported at rest revealed an association with spontaneous cognition  
516 that was characterised as verbal, thematic and deliberate ( $R = 0.213$ ,  $p = 0.008$ )  
517 (Fig. 3D). Overall, Components I and II reflected a common pattern: when  
518 regions implicated in cognitive control (inferior frontal gyrus and pre-  
519 supplementary motor area) were segregated from anterior temporal lobe and  
520 angular gyrus at rest, participants showed better performance on a range of  
521 tasks measuring semantic cognition.

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**Figure 4 The neurocognitive components of semantic task engagement. A)** Component III was characterised by reduced coupling between the angular gyrus and executive and semantic control regions, combined with stronger coupling between angular gyrus, posterior cingulate and anterior temporal lobe. This functional connectivity was associated with better performance on picture association and specific-level picture identity decisions, and poorer performance on a demanding verbal feature matching task. **B)** This neurocognitive pattern was linked to greater activity in the pre-supplementary motor area when participants viewed meaningful over meaningless sentences. **C)** Component IV on the other hand, reflected reduced connectivity between the DMN regions, which were associated with poor performance on the picture association, but good performance on the picture naming tasks. **D)** This pattern was linked to greater activity on the pre-supplementary motor area, bilateral medial occipital cortex and right insula.

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In contrast, Components III and IV related to different qualities of semantic cognition, in other words, the relative strengths and weaknesses between semantic tasks. Component III reflected relatively good performance on picture association tasks (e.g. knowing that a picture of a dog goes with a picture of a bone) and identity-matching at the specific level (e.g. matching the picture of a dog with the word Dalmatian), plus poorer performance on the feature-matching task (i.e. a difficult verbal comprehension task). At rest, individuals who scored highly on this component showed separation between the angular gyrus and inferior frontal gyrus and pre-supplementary motor area, but at the same time, they showed stronger coupling between the angular gyrus, posterior cingulate and anterior temporal lobe (Fig. 4A). Unlike Component I, this segregation of

545 inferior frontal gyrus and pre-supplementary motor area from angular gyrus did  
546 not extend to other regions in the DMN, namely anterior temporal lobe and  
547 posterior cingulate. There was, however, additional segregation of the angular  
548 gyrus from more posterior parts of posterior middle temporal gyrus, which is  
549 also implicated in semantic control. During the online presentation of semantic  
550 information in task-based fMRI, this component was associated with increased  
551 activation of a region in the pre-supplementary area (Fig. 4B). However, it was  
552 not associated with thoughts reported during the resting state scan.

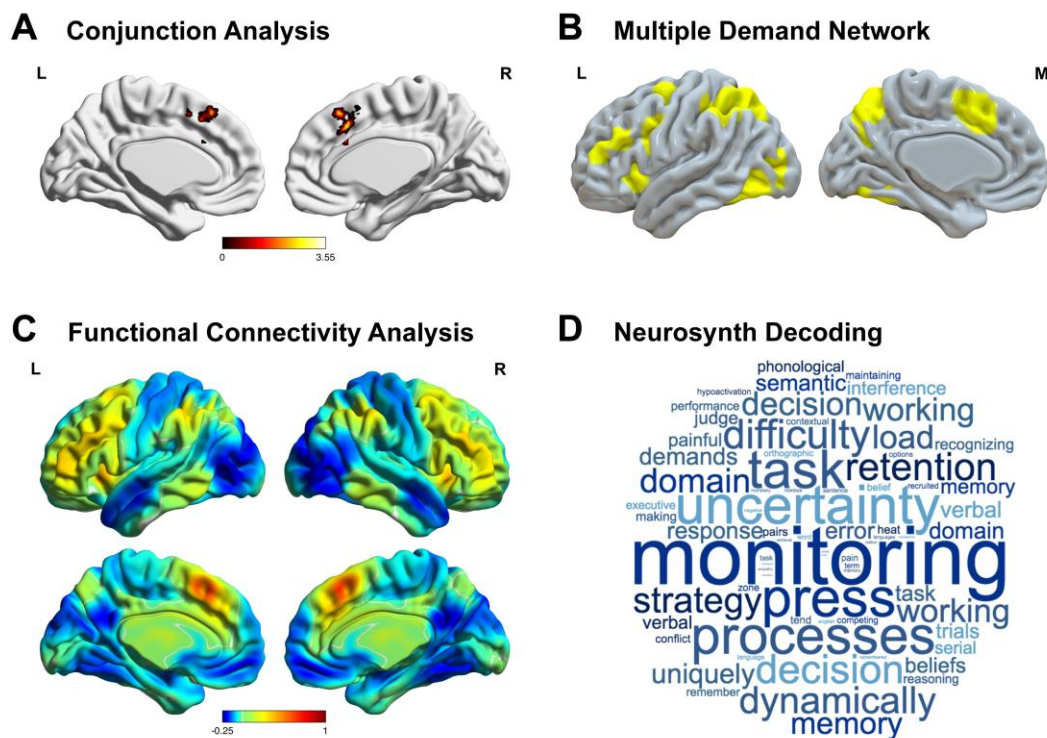
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554 Component IV described relatively good performance in two tasks involving  
555 overt speech production, picture naming and letter fluency, combined with  
556 relatively poor performance on semantic association tasks, particularly when  
557 these were presented using pictures. At rest, this component was linked to  
558 weaker coupling between nodes in the semantic system, chiefly reduced  
559 correlation between the angular gyrus and anterior temporal lobe, posterior  
560 cingulate cortex and posterior middle temporal gyrus (Fig. 4C). During the online  
561 presentation of semantic information in fMRI, this component was associated  
562 with greater activation of the pre-supplementary motor area, inferior mid-  
563 cingulate cortex, bilateral medial occipital cortex and right insula (Fig. 4D). It was  
564 not associated with the reports of thoughts at rest. Thus, in both Components III  
565 and IV, strong coupling between the anterior temporal lobe and angular gyrus at  
566 rest related to better picture comprehension, while separation of these regions  
567 was associated with better verbal semantic performance. In addition,  
568 Components III and IV shared a pattern of decoupling between angular gyrus  
569 and posterior middle temporal gyrus, and segregation of these regions at rest  
570 may be crucial for the capacity to engage successfully in externally-presented  
571 semantic tasks in the absence of strong separation between posterior cingulate  
572 cortex and frontal executive regions at rest.

573

574 Notably, our analysis highlighted a region of pre-supplementary motor area and  
575 dorsomedial prefrontal cortex, which showed greater activity during meaningful  
576 information in task-based fMRI for participants who had higher scores on three  
577 of the four components identified by CCA. To quantify this similarity, we

578 conducted a post-hoc analysis using a formal conjunction of the activation  
 579 patterns related to Components I, III and IV to reveal significant co-activation in  
 580 pre-supplementary motor area (Fig. 5A). To understand the functional  
 581 connectivity of this region, we seeded it in an independent data set available on  
 582 Neurosynth, revealing a pattern of connectivity within lateral prefrontal and  
 583 parietal regions, aspects of posterior temporal cortex and the anterior insula  
 584 (Fig. 5B). This pattern shares many features with the multi-demand network that  
 585 is implicated in performance on demanding tasks across cognitive domains (Fig  
 586 5C). This interpretation was supported by a meta-analytic decoding of the  
 587 functional connectivity map using Neurosynth, which revealed that this pattern  
 588 of connectivity was often associated with terms related to cognitive engagement  
 589 such as “monitoring”, “difficulty” and “strategy” (Fig. 5D).



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**Figure 5 Convergence across the neurocognitive components of semantic cognition. A)** Components I, III and IV all shared online activity in the semantic localiser task centered on the pre-supplementary motor area (conjunction analysis,  $Z > 2.6$ ,  $p < 0.05$ ). **B-C)** The functional connectivity of this region with the rest of the brain revealed a large-scale brain network commonly associated with regions of the multiple demand network. **D)** The decoding of this region with reverse inference using the Neurosynth database revealed a number of terms such as monitoring, strategy and decision that are often associated with demands across multiple cognitive domains.



## 599 **4. Discussion**

600

601 Our study set out to understand the relationship between emergent patterns of  
602 functional connectivity in nodes associated with semantic processing at rest and  
603 the application of semantic cognition during tasks, measured outside the  
604 scanner. We used a multivariate technique (CCA) to simultaneously decompose  
605 variability in brain and behaviour, applying an  $L_1$ -penalty that improved the  
606 interpretability of the neurocognitive components. The identified patterns of  
607 brain connectivity at rest successfully predicted task-based activation during  
608 sentence comprehension, or related to the spontaneous mental experiences of  
609 the participants during the resting-state scan. These findings support the view  
610 that individual differences in semantic cognition can be understood in terms of  
611 the balance of diverse network interactions. The findings of our study are highly  
612 coherent with component process accounts of semantic cognition (Lambon  
613 Ralph et al., 2016), since variability in semantic performance could be related to  
614 an interplay of different cognitive processes supported by distributed brain  
615 regions (see also Xu et al. (2016)).

616

617 Better performance on relatively difficult semantic tasks was associated with  
618 greater segregation at rest between regions important for cognitive control and  
619 regions in the DMN. An association between better cognitive performance and  
620 enhanced segregation between usually anti-correlated functional networks has  
621 been observed in prior studies of both executive control (Hampson et al., 2010;  
622 Kelly et al., 2008) and language. For instance, Mollo et al. (2016) found that  
623 better letter fluency performance was associated with reduced coupling between  
624 dorsal inferior frontal gyrus and retrosplenial cortex in the DMN. Building on  
625 these previous findings, our study suggests that the broad tendency to segregate  
626 regions implicated in cognitive control from the anterior temporal lobe and  
627 default mode regions at rest may relate, in general terms, to good performance  
628 on a wide range of semantic tasks.

629

630 We also found patterns of functional coupling in the brain at rest that related to  
631 each participant's relative strengths and weaknesses across the tasks in our

632 semantic battery. Specifically, Component III described a form of semantic  
633 cognition in which picture association judgements and picture-word identity  
634 matching for specific concepts were in opposition to verbal feature matching.  
635 This component was associated with stronger coupling between the angular  
636 gyrus and other regions in the DMN (anterior temporal lobe and posterior  
637 cingulate cortex), as well as weaker coupling between the angular gyrus and  
638 cognitive and semantic control regions (inferior frontal gyrus, pre-  
639 supplementary area, posterior middle temporal gyrus). Component IV described  
640 a pattern of semantic cognition in which picture naming and letter fluency was in  
641 opposition to picture association judgements. Better performance on speech  
642 production measures was associated with relative separation of posterior  
643 cingulate, angular gyrus and anterior and posterior temporal lobe regions. While  
644 Components I and II related to overall performance on semantic tasks,  
645 Components III and IV revealed qualitative differences in semantic cognition:  
646 both aspects of variability were related to the strength of coupling between brain  
647 regions across multiple networks, in line with the component process account of  
648 semantic cognition.

649

650 As well as providing evidence of the heterogeneity of semantic cognition, our  
651 study provides hypotheses about the underlying network architecture that may  
652 give rise to strengths and weaknesses on pictorial semantic tasks. Greater  
653 coupling between angular gyrus and posterior cingulate and anterior temporal  
654 cortex was associated with better relatedness judgements for pictorial stimuli in  
655 Components III and IV. This could reflect effective integration of amodal  
656 conceptual representations, thought to be formed within the anterior temporal  
657 lobe (Olson et al., 2007; Patterson et al., 2007; Zahn et al., 2007), into the core of  
658 the DMN (Andrews-Hanna et al., 2010; Bonnici et al., 2016; Yeo et al., 2011). Both  
659 posterior cingulate and angular gyrus have shown stronger responses to more  
660 imageable than concrete words in brain imaging studies (Binder et al., 2005;  
661 Sabsevitz et al., 2005; Wang et al., 2010), in contrast to other semantic and  
662 language areas such as posterior middle temporal gyrus and inferior frontal  
663 gyrus. Moreover, TMS work shows that the angular gyrus plays a critical role in  
664 specific object recognition (Davey et al., 2015) – a task that may require stronger

665 integration of visual features (e.g., stripes) to distinguish between similar  
666 concepts (e.g., horse and zebra). The posterior cingulate cortex is thought to be  
667 critical for the re-representation and global integration of diverse aspects of  
668 experience, including meaning, episodic/working memory and vision (Bzdok et  
669 al., 2015; Margulies et al., 2016; Smallwood et al., 2016; Vatansever et al., 2015a).  
670 The angular gyrus has also been described as an interface between multisensory  
671 aspects of experience and memory (Bonnici et al., 2016; Bzdok et al., 2016a;  
672 Seghier, 2013; Vatansever et al., 2016a), and is implicated in vivid recollection.  
673 Thus, aspects of semantic cognition that involve the simulation of sensory  
674 experiences may involve more integration between semantic representations in  
675 the anterior temporal lobe and the DMN (Xu et al., 2016).

676

677 There are several limitations that should be borne in mind when considering  
678 these results. First, though our ROIs were selected from a large-scale meta-  
679 analysis, there may be other regions of cortex that contribute to semantic  
680 cognition. Specifically, brain regions in the right hemisphere were omitted in this  
681 analysis. Although semantic processing is known to be strongly left-lateralised,  
682 executive control regions on the right hemisphere have been previously shown  
683 to contribute to tasks with high semantic control demands (Noonan et al., 2013).  
684 Moreover, right hemispheric brain regions has been implicated in metaphor  
685 processing (Schmidt et al., 2007) and the retrieval of broad semantic connections  
686 (Jung-Beeman et al., 2004). However, such triaging procedure was necessary to  
687 improve the interpretability of our results and to solve the limitations associated  
688 with the CCA technique. Notably, exclusion of the right-hemisphere helped us  
689 overcome the limitations on the number of seeds that could be entered into CCA,  
690 depending on the available sample size. In addition, there may be important  
691 aspects of semantic processing that we did not capture in our battery of tasks. As  
692 a consequence, our data provide evidence for brain connectivity patterns that  
693 relate to quantitative and qualitative varieties of semantic cognition, but we  
694 cannot specify the exact number of the varieties of semantic cognition in full.  
695 Furthermore, our implementation of CCA imposed orthogonality between the  
696 latent components (Witten et al., 2009). In other words, the aspects of functional  
697 connectivity and behavioural patterns that would be shared between the factors

698 of variation in the population are largely collapsed into the components by the  
699 present analysis that focuses mainly on finding components that do correlate  
700 with each other only to the least possible extent. Nevertheless, it should be noted  
701 that although the optimization goal of CCA is to have components as  
702 uncorrelated as possible, this procedure does not guarantee zero correlation.  
703 This is because regularised CCA does not force strict orthogonality in order to  
704 avoid overfitting (Melzer et al., 2003). In summary, though similar  
705 decomposition methods (such as PCA) has been successfully used as models in  
706 psychological research, the existing caveats analogously also apply here to our  
707 CCA components, which will require further investigation and optimisation.

708

709 Moreover, our study examined individual differences in patterns of brain  
710 connectivity solely at rest. However, it is possible that connectivity during task  
711 states will also relate to differences in semantic cognition between individuals –  
712 and these network interactions are likely to differ in substantial ways from those  
713 described here (Krieger-Redwood et al., 2016; Vatansever et al., 2015a, b). For  
714 instance, we observed more activation of pre-supplementary motor area during  
715 semantic processing in task-based fMRI both for participants who were generally  
716 good at semantic tasks (and who strongly separated default mode and executive  
717 areas at rest in general terms) and for participants who showed an uneven  
718 profile of relatively better or worse performance on different tasks (and who  
719 separated angular gyrus from a region linked to semantic control in posterior  
720 middle temporal gyrus). Thus, some degree of functional separation at rest  
721 between default mode and control regions may support the capacity to flexibly  
722 reorganise cognition to engage with a task (Vatansever et al., 2016b). The  
723 recruitment of pre-supplementary motor area could reflect general task  
724 engagement, consistent with the contribution of this region to the multiple-  
725 demand network (Duncan, 2010). This prediction needs to be explored in future  
726 studies by applying a similar decomposition approach to task-based fMRI data.

727

728 Our data also provides insight into the contribution of semantic processes to the  
729 generation of unconstrained thoughts at rest (Binder et al., 2009; Binder et al.,  
730 2003; Smallwood et al., 2016). A pattern of strong coupling of the anterior

731 temporal lobe and angular gyrus with inferior frontal gyrus and pre-  
732 supplementary area predicted reports of verbal, thematic and deliberate  
733 thoughts at rest (Component II). This finding is consistent with the view that  
734 self-generated thoughts rely on the same component processes as external tasks  
735 and supports a role for control processes in the coordination of some aspects of  
736 spontaneous thought (Bzdok et al., 2016b; Smallwood, 2013; Smallwood and  
737 Schooler, 2015). Participants who showed too much coupling between nodes of  
738 the DMN and the executive system may have failed to engage with our external  
739 tasks, consistent with studies showing that mind-wandering is linked to poor  
740 task performance (Mooneyham and Schooler, 2013).

741

## 742 **5. Conclusions**

743

744 Overall, the results of this study provide compelling evidence for the component  
745 process account of semantic cognition. The results suggest that different patterns  
746 of connectivity between large-scale brain networks show relationships to both  
747 quantitative and qualitative variability in semantic cognition. Further studies  
748 exploring the basis of these neurocognitive components will not only illuminate  
749 the underlying neural mechanisms in this domain, but will also pave the way for  
750 improving our understanding of semantic impairments in disease states.

751

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753

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