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

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Abstract

1
2 Contemporary theories assume that semantic cognition emerges from a neural
3 architecture in which different component processes are combined to produce
4 aspects of conceptual thought and behaviour. In addition to the state-level,
5 momentary variation in brain connectivity, individuals may also differ in their
6 propensity to generate particular configurations of such components, and these
7 trait-level differences may relate to individual differences in semantic cognition.
8 We tested this view by exploring how variation in intrinsic brain functional
9 connectivity between semantic nodes in fMRI was related to performance on a
10 battery of semantic tasks in 154 healthy participants. Through simultaneous
11 decomposition of brain functional connectivity and semantic task performance,
12 we identified distinct components of semantic cognition at rest. In a subsequent
13 validation step, these data-driven components demonstrated explanatory power
14 for neural responses in an fMRI-based semantic localiser task and variation in
15 self-generated thoughts during the resting-state scan. Our findings showed that
16 good performance on harder semantic tasks was associated with relative
17 segregation at rest between frontal brain regions implicated in controlled
18 semantic retrieval and the default mode network. Poor performance on easier
19 tasks was linked to greater coupling between the same frontal regions and the
20 anterior temporal lobe; a pattern associated with deliberate, verbal thematic
21 thoughts at rest. We also identified components that related to qualities of
22 semantic cognition: relatively good performance on pictorial semantic tasks was
23 associated with greater separation of angular gyrus from frontal control sites
24 and greater integration with posterior cingulate and anterior temporal cortex. In
25 contrast, good speech production was linked to the separation of angular gyrus,
26 posterior cingulate and temporal lobe regions. Together these data show that
27 quantitative and qualitative variation in semantic cognition across individuals
28 emerges from variations in the interaction of nodes within distinct functional
29 brain networks.

30

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 mm³, 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/CorticalParcel%20lotion_Yeo2011)
283 /fswiki/CorticalParcel lotion_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.

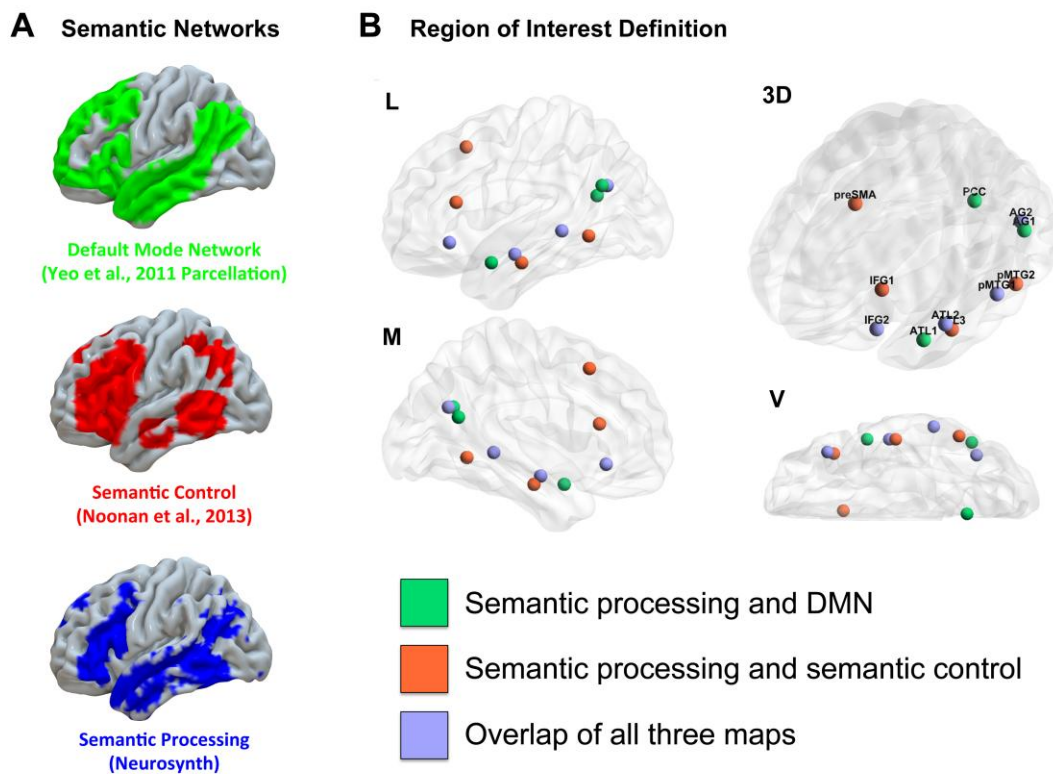
290

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**

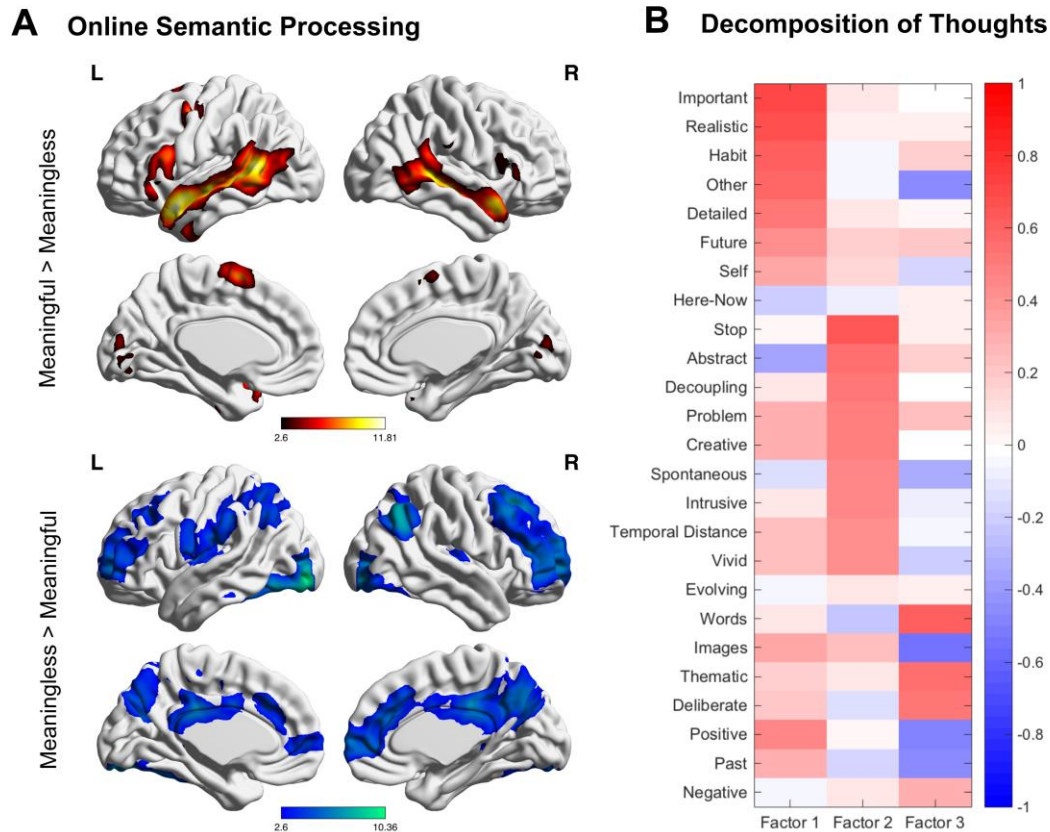
357 Similar to other commonly used decomposition techniques in neuroimaging (e.g.
358 ICA or PCA), biologically meaningful number of CCA components is determined
359 by external knowledge. In other words, the number of viable components are
360 usually determined by the level at which the components 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

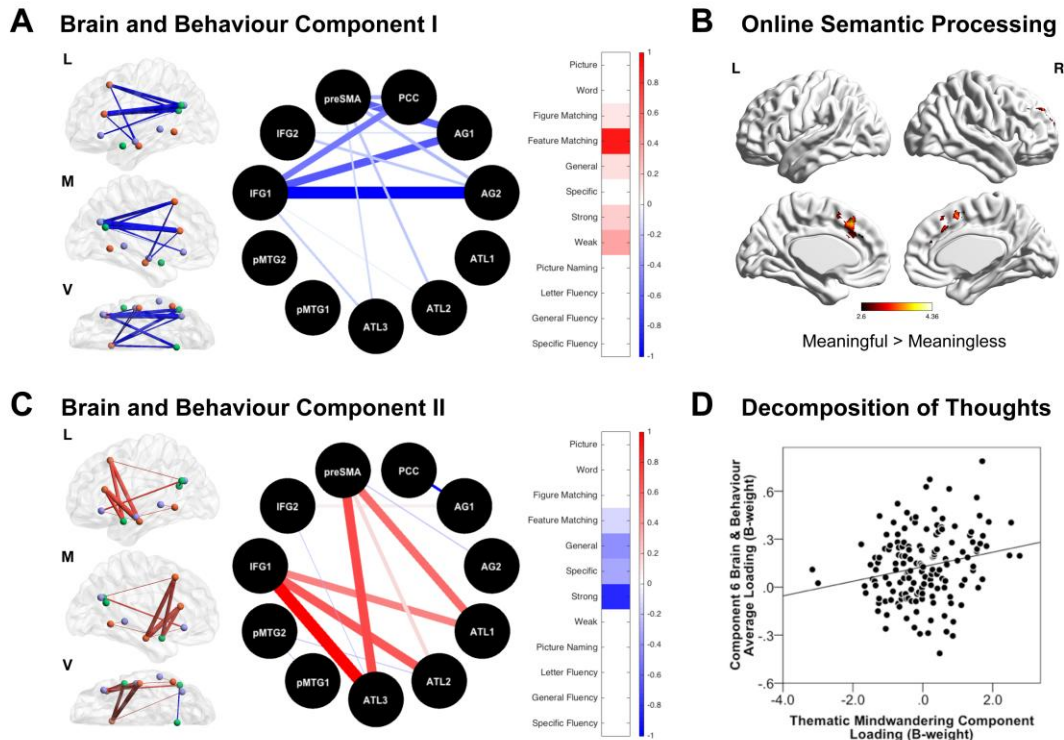
456 which construct validity was demonstrated through a relationship with other
 457 measures relevant to semantic cognition. The canonical correlations and the
 458 squared canonical correlated for these four components were 0.25 ($p = 0.002$),
 459 0.20 ($p = 0.012$), 0.08 ($p = 0.322$), 0.19 ($p = 0.016$) 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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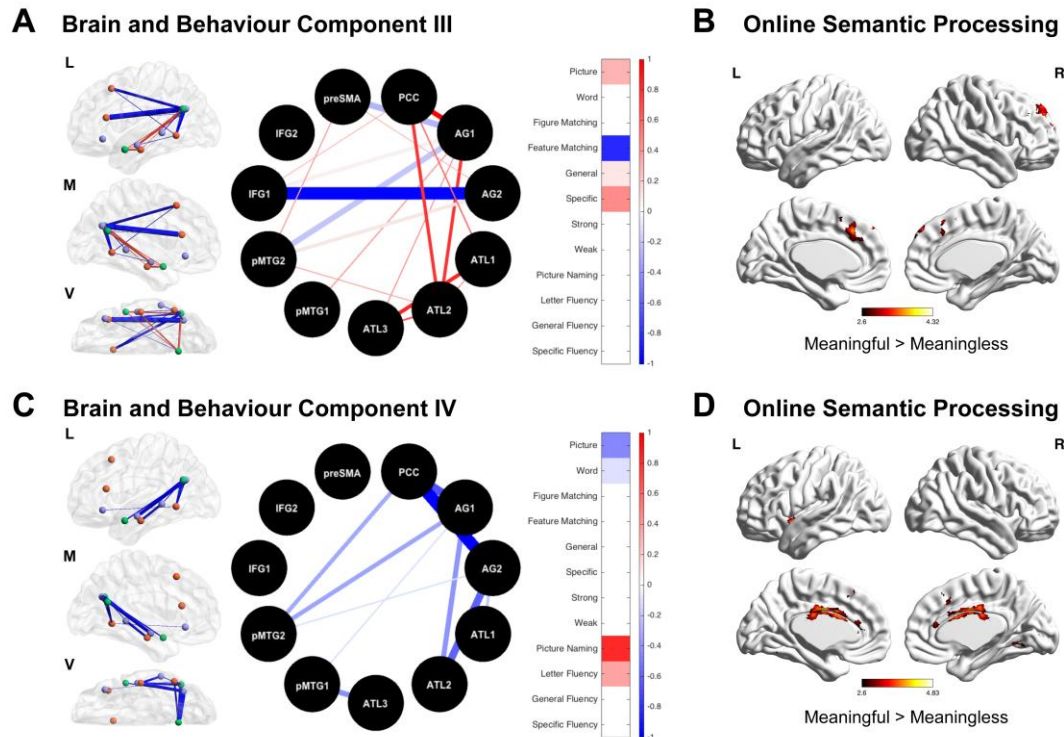
Figure 3 Neurocognitive components related to global performance in semantic cognition. The brain connectivity patterns based on the identified canonical components are displayed on an MNI152 glass brain in three different planes: lateral (L), medial (M) and ventral (V), as well as in a circular representation. 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.

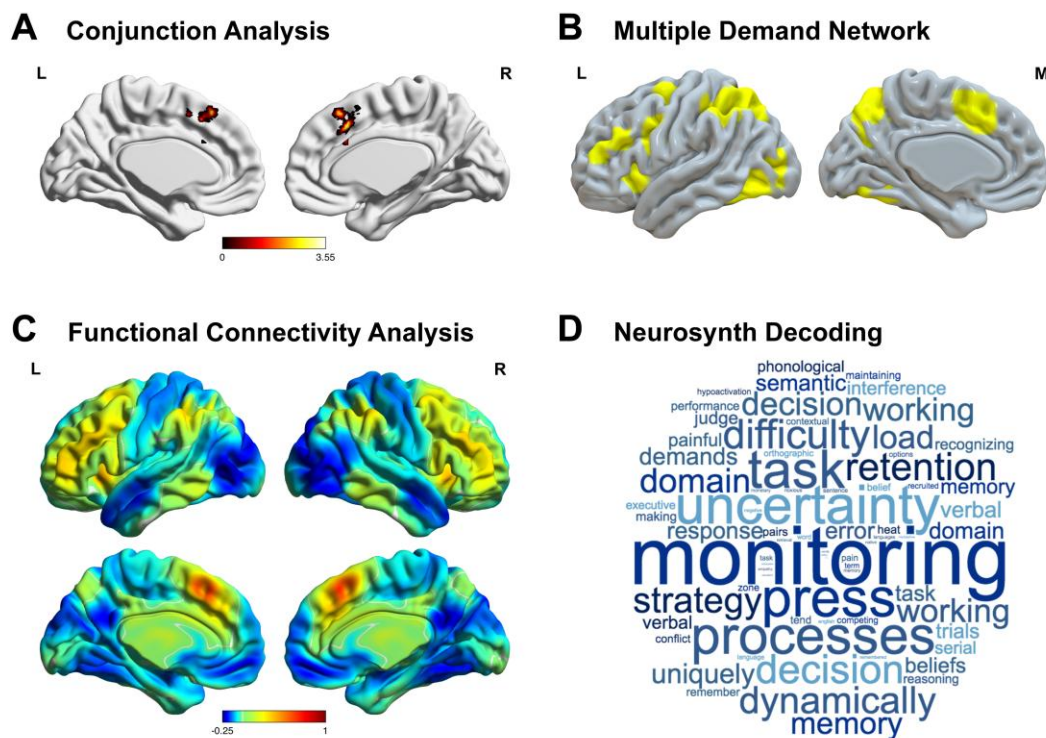
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554 Component IV described relatively good performance in two tasks involving
555 overt speech production, picture naming and letter fluency, combined with
556 relatively poor performance on semantic association tasks, particularly when
557 these were 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.

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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).



590

591

592 **Figure 5 Convergence across the neurocognitive components of semantic cognition.** A) Components I,
 593 III and IV all shared online activity in the semantic localiser task centered on the pre-supplementary motor
 594 area (conjunction analysis, $Z > 2.6$, $p < 0.05$). B-C) The functional connectivity of this region with the rest of
 595 the brain revealed a large-scale brain network commonly associated with regions of the multiple demand
 596 network. D) The decoding of this region with reverse inference using the Neurosynth database revealed a
 597 number of terms such as monitoring, strategy and decision that are often associated with demands across
 598 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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762 7. References

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