

1 **Incidental Verbal Semantic Processing recruits the fronto-temporal**  
2 **semantic control network**

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20 **ABSTRACT.**

21 *The fronto-parietal semantic network, encompassing the inferior frontal gyrus and the posterior*  
22 *middle temporal cortex, is considered to be involved in semantic control processes. The explicit vs*  
23 *implicit nature of these control processes remains however poorly understood. The present study*  
24 *examined this question by assessing regional brain responses to the semantic attributes of an*  
25 *unattended stream of auditory words while participants' top-down attentional control processes*  
26 *were absorbed by a demanding visual search task. Response selectivity to semantic aspects of verbal*  
27 *stimuli was assessed via an fMRI response adaptation paradigm. We observed that implicit*  
28 *semantic processing of an unattended verbal stream recruited not only unimodal and amodal cortices*  
29 *in posterior supporting semantic knowledge areas, but also inferior frontal and posterior middle*  
30 *temporal areas considered to be part of the semantic control network. These results indicate that*  
31 *fronto-temporal semantic networks support incidental semantic (control) processes.*

32

33 **Keywords:** "IFG" incidental" "pMTG" "repetition suppression ""semantic control"

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## 36 **Introduction**

37 Semantic cognition refers to a range of cognitive processes and representations encoded in  
38 distributed brain areas (Binder et al. 2009; Price 2012) that define our knowledge of objects, word  
39 meanings, facts and people (Ralph et al. 2016a). An influential model, the controlled semantic  
40 cognition (CSC) framework (Ralph et al. 2016a; Chiou et al. 2018; Thompson et al. 2018; Jefferies et  
41 al. 2020), posits that semantic cognition relies on the interaction between semantic representations  
42 on the one hand, and their control on the other (Ralph et al. 2016a). Semantic knowledge involves  
43 specific, low-level as well as generalizable high-level, relationships between sensory, motor, linguistic  
44 and affective features as well as their integration. Semantic control allows the manipulation of these  
45 representations and to generate context-specific semantic inferences based on interactions between  
46 modality-specific sources of information (Lambon Ralph, Sage, et al. 2010).

47 These two aspects of semantic cognition systems are supported by distinct neural networks.  
48 Semantic knowledge is supported by modality-specific distributed neocortical regions which  
49 bidirectionally communicate with transmodal hubs located within the anterior temporal lobes (ATL)  
50 (Lambon Ralph, Cipolotti, et al. 2010; Ralph et al. 2016a) and for some the angular gyrus (AG)  
51 (Noppeney et al. 2004; Ruff et al. 2008; Jefferies et al. 2020). Note that for other authors, the AG  
52 appears to serve a more domain-general function such as a multimodal online buffer for incoming  
53 internal or external information (Humphreys and Lambon Ralph 2015; Humphreys et al. 2015).

54 The ‘semantic control’ system relies primarily on the inferior frontal gyrus (IFG) and the posterior  
55 middle temporal gyrus (pMTG) (Thompson-Schill et al. 1999; Badre and Wagner 2005; Rodd et al.  
56 2005; Jefferies and Lambon Ralph 2006; Binder et al. 2009; Noonan et al. 2010; Seghier et al. 2010;  
57 Davey et al. 2016; Jefferies et al. 2020). This system is thought to monitor and modulate the activity  
58 of semantic knowledge areas (Devlin et al. 2003; Yarkoni et al. 2011; Huang et al. 2012; Jefferies  
59 2013; Zhu et al. 2013; Della Rosa et al. 2018) and may adapt itself when one or more of the CSC  
60 components are compromised by damage, with IFG and pMTG being able to mutually compensate

61 for their failure, or in case of demanding tasks (Jefferies 2013; Davey et al. 2015; Ralph et al. 2016a;  
62 Hallam et al. 2018; Jefferies et al. 2020).

63 Neural substrates of both unimodal and multimodal semantic representations have been shown to  
64 be recruited by preconscious stimuli, suggesting that semantic knowledge can be processed under  
65 conditions of reduced or even absent awareness (Perrin et al. 2002; Gaillard et al. 2006; Kouider and  
66 Dehaene 2007). By contrast, semantic control is generally believed to rely on conscious processes  
67 and is generally assessed by tasks involving explicit judgment and decision making processes (Ralph  
68 et al. 2016a; Jefferies et al. 2020) although the amount of semantic control has sometimes been  
69 manipulated in a less explicit manner (Badre and Wagner 2002). Some authors have also considered  
70 the theoretical possibility of automatic control process (Badre and Wagner 2005; Davey et al. 2015).

71 These control processes, supported by the IFG, are further believed to exert a top-down influence  
72 onto unimodal semantic representation areas (Chiou et al. 2018). However, the possibility remains  
73 that semantic control processes may also be at least partially independent of explicit control  
74 processes. Indeed patients with semantic control deficits can show increased effects of semantic  
75 interference and intrusion errors when no explicit semantic judgment is required: when repeatedly  
76 naming pictures from the same versus a different semantic category, these patients show increased  
77 semantic interference effect relative to healthy controls (Schnur et al. 2006; Hamilton and Martin  
78 2007). It could however be argued that this task, although not directly involving explicit semantic  
79 control in the form of semantic judgment, may however be considered as an explicit task as the  
80 participants have to produce a target response in a top-down manner. Currently, we do not know  
81 whether the semantic control network involves purely explicit semantic control processes or  
82 whether it can also be recruited incidentally.

83 We addressed this question by assessing brain responses to semantic information using an incidental  
84 semantic activation paradigm. Regional brain responses to the semantic attributes of an unattended  
85 auditory word stream were recorded while the participants' attentional control was monopolized by  
86 a demanding visual search task in which participants had to detect an open circle among full circles

87 and then indicate the location of the aperture (see Figure 1). This task is considered to demand a  
88 high degree of visual selective attention, decision making and motor control (Davis and Palmer 2004;  
89 Ettenhofer et al. 2016; Schill et al. 2020). Neural sensitivity to semantic processing was assessed  
90 using an fMRI response adaptation paradigm (also known as repetition suppression) (Grill-Spector  
91 2006; Garrido et al. 2009; Larsson and Smith 2012). This phenomenon refers to the reduction of local  
92 brain responses to repeated presentation of a specific stimulus type or attribute (Grill-Spector and  
93 Malach 2001; Sayres and Grill-Spector 2006). Representational areas have been shown to present  
94 such a repetition adaptation of neural responses during same semantic family word presentation  
95 (Chouinard et al. 2008; Yee et al. 2010; Menenti et al. 2012). In this study, we aimed to determine  
96 whether response adaptation in semantic representational areas would also be obtained by purely  
97 incidental semantic stimulation, when no semantic information is processed in a conscious and  
98 voluntary manner. Here, while the participants were carrying out the visual search task, auditory  
99 blocks of 5 to 7 words from the same semantic category (tools, clothes, colors, or animals) were  
100 presented (see Figure 1). We reasoned that brain areas sensitive to semantic processing of the word  
101 stream would decrease their response during the presentation of a given homogenous semantic  
102 block and increase again at the beginning of the following block.

103 Second, we aimed to determine if semantic control-associated regions would also show such  
104 repetition adaptation effects during incidental semantic processing, in the absence of any 'active'  
105 engagement of semantic or other control processes. Most studies investigating semantic control so  
106 far used explicit judgment tasks implying active control processes (Badre et al. 2005; Ralph et al.  
107 2016b; Jefferies et al. 2020) whereas in everyday life semantic control is used in a more incidental  
108 manner such as understanding spontaneously in a conversation that 'spilling the beans' has nothing  
109 to do with food.

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## 113 **Materials and methods**

### 114 **Participants**

115 Fourteen healthy right-handed volunteers (age range 18-26 y., 8 females) gave their written informed  
 116 consent to participate in this study and received a financial compensation. They were non-smokers,  
 117 native French-speakers, had normal audition and normal or corrected-to-normal vision. They had not  
 118 any history of medical, neurological or psychiatric disorders. The study was approved by the Ethics  
 119 Committee of the Faculty of Medicine of the University of Liège.

### 120 **Experimental design**

121 Participants were told that they participated in an fMRI study focusing on visual attention, which  
 122 implied performing a demanding visual search task in a noisy environment (Figure 1). In this task, each  
 123 trial consisted of the 1500ms display of 15 to 20 randomly distributed circles (2cm diameter,  
 124 distributed over a 20 x 20 area). All of them were complete except one which was open by 6,2° at  
 125 random angle. Participants were instructed to specify whether the circle opening was left or right-  
 126 handed. When the opening was at the top or the bottom of the circle, the opening side was left free  
 127 to decide by participants. Simultaneously, verbal stimuli, presented as distractors, were delivered  
 128 through headphones. Frequent, concrete, imageable and unambiguous French words, 1 to 3-syllable  
 129 long, were selected based on their frequency of occurrence in the usual oral language (> 500 of litteral  
 130 frequency, as assessed by BRULEX index (Pagel et al. 1998), from four semantic categories (tools,  
 131 clothes, colours, animals). Homophone and polysemic words were discarded (see Table 1).

132 **Table 1.** *Presented words by semantic family (in French).*

133

<b>TOOLS</b>	<b>CLOTHES</b>	<b>COLOURS</b>	<b>ANIMALS</b>
Marteau	Veste	Rouge	Biche
Ciseaux	Pantalon	Bleu	Ecureuil
Fourche	Soulier	Vert	Lapin
Pince	Bonnet	Jaune	Tigre
Scie	Echarpe	Blanc	Mouche
Pelle	Robe	Noir	Lion
Pioche	Jupe	Mauve	Singe

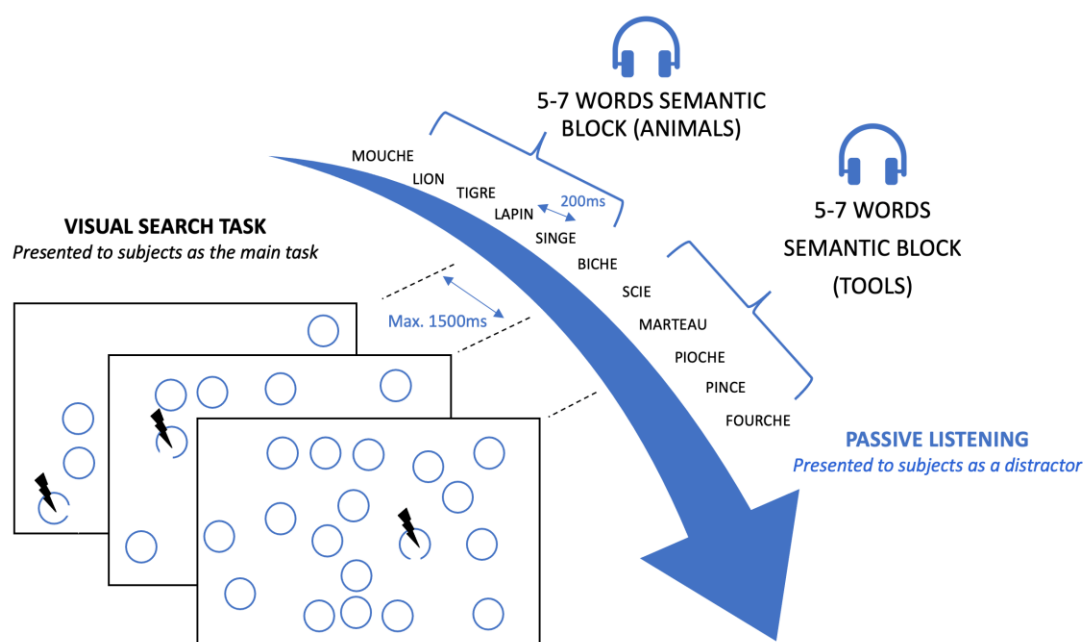
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135

136 The words were prerecorded by a male speaker and presented in blocks of 5 to 7 words from the same  
 137 semantic category, at the rate of one word every 2000 ms. Each word was presented several times,  
 138 with an equal probability to occur in any position within the semantic block. The block themselves  
 139 were presented in a random order. Each run lasted 3 to 5 minutes according to the number of  
 140 presented words and 3 runs were repeated in a row within the MR scanner, with interleaved 3 to 5-  
 141 minute resting periods (see Figure 1).

142

143 **Figure 1.** Schematic representation of experimental design.



144

145

146 After the MRI sessions, participants were debriefed using questionnaires successively probing their  
 147 feelings about the visual task and their feedback, then assessing their comfort and their perception of  
 148 the “background noise”, the words that they heard, the words that they were able to remember and  
 149 finally, whether they identified any structure in the word stream. This assessment was meant to  
 150 exclude subjects who may have had an explicit identification of the semantic nature of the stimuli as

151 they may not have focused exclusively on the visual search task. A debriefing questionnaire further  
152 assessed of the covert nature of the stimuli and the level of attention paid by participants to the  
153 auditory material as well as to the visual display (see Results for further information).

#### 154 Recordings.

155 Data were acquired with a 3 T head-only magnetic resonance (MR) scanner (Siemens MAGNETOM  
156 Allegra) using a gradient echo-planar sequence [Gradient echo-planar (EPI) axial slice orientation  
157 whole brain/most of the brain, 34 slices, FoV = 192 x 192 mm<sup>2</sup>, voxel size 3 x 3 x 3 mm<sup>3</sup>, 25% interslice  
158 gap, matrix size 64 x 64 x 34, TR = 2040ms, TE = 30ms, Flip Angle = 90°]. In all sessions, the first three  
159 volumes were discarded to account for magnetic saturation effects on brain tissue. A structural MR  
160 scan was acquired at the end of the experimental session (T1-weighted three-dimensional  
161 magnetization-prepared rapid-acquisition gradient echo sequence; TR, 1960 ms; TE, 4.43 ms; inversion  
162 time, 1100 ms; FOV, 230 × 173 mm<sup>2</sup>; matrix size, 256 × 192 × 176; voxel size, 0.9 × 0.9 × 0.9 mm).  
163 Stimuli were displayed using a video projector on a screen positioned at the rear of the scanner, which  
164 the subject could comfortably see through a mirror mounted on the standard head coil. The responses  
165 of the subjects to the distracting visual task were recorded using a small MRI compatible keyboard.

#### 166 Data analysis.

167 Data processing and all statistical analyses were performed with the Statistical Parametric Mapping  
168 SPM8 software package (Wellcome Trust Centre for Neuroimaging, London UK,  
169 <http://www.fil.ion.ucl.ac.uk/spm/>) implemented in MATLAB (MathWorks Inc., Sherborn, MA). All  
170 functional volumes were spatially realigned, unwarped, normalized to MNI space using the unified  
171 segmentation procedure of SPM8, and smoothed (Gaussian kernel 8mm Full Width at Half Maximum,  
172 FWHM).

173 The analysis conformed to a mixed effects analysis and accounted for fixed and random effects (RFX).  
174 For each subject, a general linear model was used to estimate brain responses at each voxel. Trials  
175 corresponding to events of the 4 semantic categories (tools, clothes, colors, animals) as well as events  
176 of the visual search task were modelled as stick functions and convolved with the canonical



177 hemodynamic response function.

178 A further regressor modelled the influence of a linear adaptation of BOLD response on word processing  
179 within semantic blocks, assigning a value of 7 for the first word of the block, 6 for the second, 5 for the  
180 third, and so forth. Movement parameters and a constant parameter were also included as covariates  
181 in the design matrix.

182 High-pass filtering was implemented in the matrix design using a cut-off period of 128 s to remove  
183 slow drifts from the time series. Serial correlations in the fMRI signal were estimated using an  
184 autoregressive (order 1) plus white noise model and a restricted maximum likelihood (ReML)  
185 algorithm.

186 Linear contrasts assessed: (1) within-block response adaptation to all semantic stimuli (versus  
187 baseline), (2) within-block response adaptation to words of each semantic category (C= colours, V=  
188 clothes, A= animals and O = tools) in comparison to all the others, and (3) the response adaptation of  
189 words across the whole scanning session.

190 Summary statistics images were smoothed (Gaussian kernel, 6 mm FWHM) and entered in the RFX  
191 analysis. Statistical inferences were performed at the cluster level at  $p < 0.05$ , with familywise error  
192 corrections for multiple comparisons across the entire brain volume, with a cluster-forming threshold  
193 of  $p < 0.001$  uncorrected; this procedure has been shown to minimize the likelihood of false positives  
194 (Eklund et al. 2016). For the ROI analyses, the threshold was also defined at  $p < 0.05$  with small volume  
195 familywise error corrections based on Gaussian random field theory over small spherical volumes (10  
196 mm radius) located in structures of interest reported in the literature focusing on semantic processing  
197 and semantic cognition. These ROI were defined based on the average coordinates published in the  
198 literature and involving the angular gyrus (AG) (Seghier et al. 2010), the temporal poles, the lingual  
199 and fusiform gyri (Dehaene et al. 2002; Jefferies and Lambon Ralph 2006; Ruff et al. 2008; Binney et  
200 al. 2010; Price 2010a; Seghier and Price 2012; Ulrich et al. 2015; Teige et al. 2018). We further  
201 considered the anterior superior temporal gyrus (STG) as this part has also been associated with access

202 to semantic knowledge (Ruff et al. 2008; Visser and Lambon Ralph 2011; Rämä et al. 2012; Hallam et  
203 al. 2018). For the semantic control framework, ROIs involved the IFG and pMTG based on the spatial  
204 coordinates published by Jefferies et al. and Badre. *A priori* locations of interest were the following:  
205 AG [-47, -59, 25] (Price 2010a) and [-30, -64, 24] (Price 2010a; Seghier et al. 2010; Seghier and Price  
206 2012; Price et al. 2015), ATL [-38, 18, -24] (Damasio et al. 2004; Visser et al. 2012; Rice et al. 2015),  
207 right ATL [40, 24, -33] (Price 2010b; Visser et al. 2012), fusiform gyrus [-30, -70, -10] (Dehaene et al.  
208 2002; Jefferies and Lambon Ralph 2006; Ruff et al. 2008; Binney et al. 2010; Price 2010a; Seghier and  
209 Price 2012; Ulrich et al. 2015; Teige et al. 2018), STG [-46, -6, -10] (Ruff et al. 2008; Visser and Lambon  
210 Ralph 2011; Rämä et al. 2012; Hallam et al. 2018), IFG [-54, 18, 8] and pMTG [-56, -50, 3] (Badre et al.  
211 2005; Whitney et al. 2011; Teige et al. 2018)]. Stereotactic coordinates refer to the MNI space.

212 We also investigated functional connectivity between activity in the left IFG and distant brain regions  
213 involved in semantic processing. Using psychophysiological interaction (Friston et al. 1997; Gitelman  
214 et al. 2003) we determined to which extent category-specific processing regions interacted with the  
215 semantic control network.

216 After defining the contrasts of interest, BOLD signals were extracted from the seed region of interest  
217 (Left IFG) of each subject. A new linear model was then constructed for each participant, using three  
218 regressors: the covert listening condition of interest (e.g., animal names), the activity in the reference  
219 area, and the interaction of interest between the first (psychological) and second (physiological)  
220 regressors. Standard psychophysiological (PPI) analyses were carried out for each subject using the  
221 Generalized PPI toolbox (McLaren et al. 2012). These contrast images were then entered in a second-  
222 level (random effects) analysis. A one-sample t-test was performed to assess the functional  
223 connectivity pattern during passive listening for each semantic family separately (cluster level at  $p <$   
224 0.05, with familywise error corrections for multiple comparisons across the entire brain volume, with  
225 a cluster-forming threshold of  $p < 0.001$  uncorrected. For the ROIs the threshold was defined at  $p <$   
226 0.05 with small volume familywise error corrections over small spherical volumes (10 mm radius)

227 located in structures of interest reported in the literature focusing on semantic processing and  
228 semantic cognition).

229

## 230 **Results.**

### 231 Behavioral results

232 All subjects performed the task with relatively high accuracy (mean  $72.4 \pm 8$  % hits), suggesting that  
233 participants focused on the visual task as instructed. At debriefing, none was aware that words were  
234 organized by semantic categories although most participants could recall a few words ( $5.61 \pm 1.06$   
235 words, out of 28). Participants also reported strong engagement in the visual search task as they  
236 described their behaviour as 'focused' to 'very focused' for this task. Participants described the visual  
237 task as 'demanding' to 'very difficult', and the background noise as 'not bothering' to 'slightly  
238 bothering'. Most of them appeared to have been more disturbed by the MRI noise itself. They were  
239 unable to reliably identify presented words among other words in a list (mean identification:  $6.12 \pm$   
240  $1.9$  out of 28 target words presented together with non-target words in a complete list of 40 words).  
241 Finally, when asked to cite five animal, tool or clothes names, subjects produced very few words that  
242 had been presented during the experimental task in the scanner. For clothes an average of  $1,2 \pm 0.5$   
243 names were identical to one of presented words; for animals, this number was  $1.1 \pm 0.4$  identical and  
244 for tools it was  $0.8 \pm 0.3$ . Colour words were not assessed given the limited number of color words that  
245 can be produced.

246

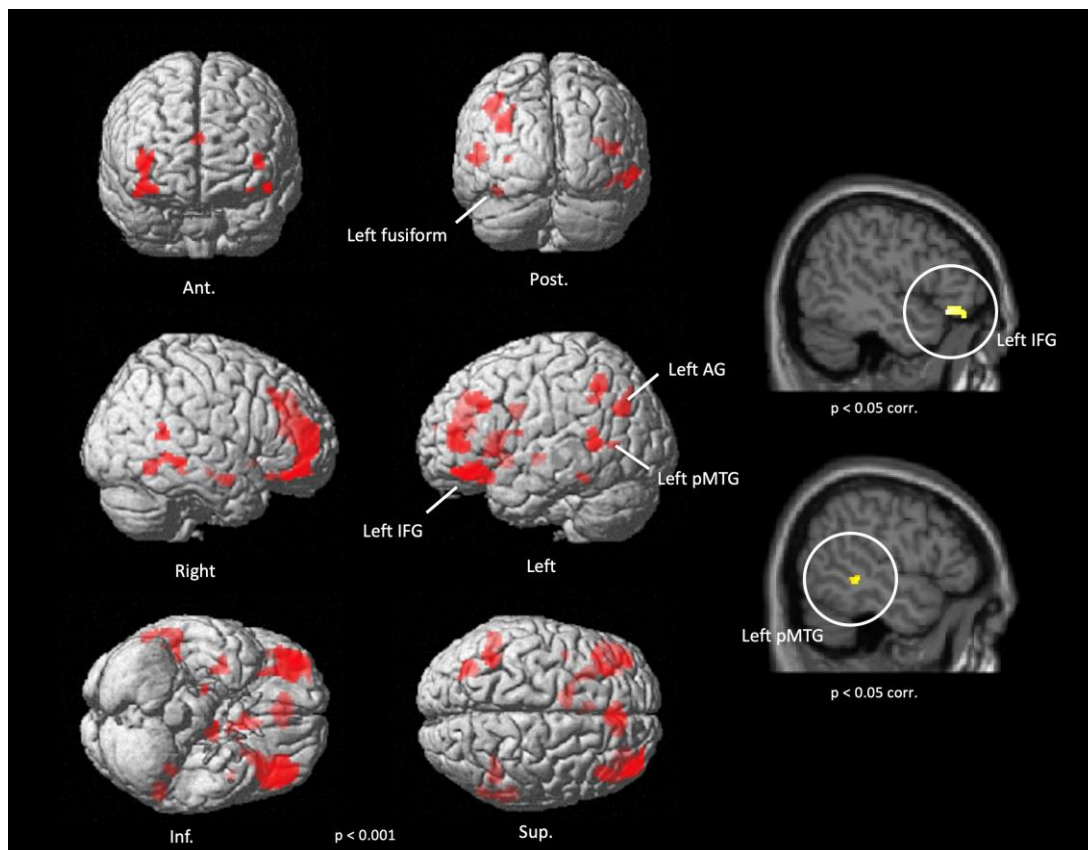
### 247 Functional MRI results

248 Within-block adaptation to semantic stimuli (irrespective of semantic categories) elicited significant  
249 activation of several clusters (see Table 3) in both the semantic representation amodal network (right  
250 ATL, left AG, left thalamus, left fusiform gyrus, left cingulate gyrus, left caudate nucleus and left STG)  
251 and the semantic control network (left IFG and left pMTG). This was also support when considering  
252 response adaptation across the entire scanning session: again, irrespective of semantic category,

253 response adaptation was observed in both IFG and pMTG ROIs, in addition to temporo-parietal ROIs  
 254 of the semantic representation amodal network (see table 4 and figure 2).

255

256 **Figure 2.** *Semantic-related adaptation activations throughout scanning session – All semantic*  
 257 *categories included.*



258

259

*The results are shown at a statistical of  $p < 0.001$  uncorrected, or  $p < 0.05$  FWE corrected over SVC.*

260

261 For assessing adaptation responses to specific semantic categories, we contrasted one semantic  
 262 family to all others (e.g., tool names activations minus animal, color and cloth names). Within-block  
 263 specific adaptation to tool names (versus all other categories) was associated with significant activity  
 264 foci in left AG, left superior temporal gyrus, motor cortex, right ITG and left fusiform gyrus when  
 265 compared to other semantic categories (Table 2, Figure 3). Activity foci for within-block adaptation  
 266 associated with animal names (versus all other categories) involved the left AG, left hippocampus,  
 267 bilateral precuneus and the left caudate nucleus (Table 2, Figure 3). For color names versus all other

268 categories, significant within-block adaptation was detected in the right fusiform gyrus, right  
 269 hippocampus, left posterior hippocampus, and left striatum. (Table 2, Figure 3).

270

271 **Table 2.** *Within-semantic block adaptation – Specific semantic categories.*

272

	<i>MNI coordinates</i>			<b>z score</b>
	<b>x</b>	<b>y</b>	<b>z</b>	
<b>TOOLS</b>				
Left angular gyrus	-22	-78	16	3.25
Right ITG	54	-4	-14	3.23
Left STG	-40	-12	-20	2.84
Left fusiform gyrus	-20	-74	-4	4.03
Left motor cortex	-30	-48	40	3.00
Left precuneus	-35	-32	36	2.89
<b>ANIMALS</b>				
Left angular gyrus	-46	-70	24	2.85
Left hippocampus	-24	-4	-28	2.95
Right precuneus	12	-50	50	3.36
Left caudate nucleus	-22	-22	20	3.20
Left precuneus	-10	-40	40	3.24
<b>COLOURS</b>				
Right fusiform gyrus	8	-80	-2	3.63
Left post. hippocampus	-34	-36	2	3.17
Right hippocampus	28	-34	-18	4.03
Left striatum	-28	-12	2	3.20
<b>CLOTHES</b>				
Left angular gyrus	-28	-81	28	3.90
Left thalamus	-4	-2	0	3.35
Right mid. cingulate gyrus	8	-4	32	3.94
Right ATL	30	14	-34	3.22

*ITG = inferior temporal gyrus, STG = superior temporal gyrus, pMTG = posterior middle temporal gyrus, ATL = anterior temporal lobe.*

*Significant at  $p < 0.05$  corr. over SVC. All coordinates refer to MNI space.*

273 Selective within-block adaptation to cloth names (versus all others) was significant in left AG, left  
 274 thalamus, right middle cingular gyrus and right ATL (Table 2, Figure 3). Overall, these results show  
 275 that semantic processing areas were selectively and automatically recruited by covert auditory  
 276 stimuli in the same way they transmodally encode conceptual representations of concrete objects  
 277 and their properties in overt studies (Thompson-Schill 2003; Wheatley et al. 2005; Barsalou 2008;  
 278 Kiefer and Pulvermüller 2012) with a differentiation of a dorsal stream (involved in the

279 representations of semantics related to movements and actions and a ventral stream (involved in the  
 280 semantic representation of shapes and color (Bartels and Zeki 2000; Hubbard et al. 2011; Perlman et  
 281 al. 2011; Weiner and Zilles 2016; Neudorf et al. 2019), and a more general involvement of left AG  
 282 which has been regarded as a thematic hub for semantic representation (Lewis et al. 2019) as well as  
 283 essential for automatic retrieval of specific semantic information (Davey et al. 2015; Jefferies et al.  
 284 2020) or more recently as a multimodal ‘automatic’ buffer (Humphreys and Lambon Ralph 2015;  
 285 Humphreys et al. 2015).

286 **Table 3.** *Within-semantic block adaptation – All semantic categories included.*  
 287

Area	MNI coordinates			z score
	x	y	z	
Left angular gyrus	-40	-74	32	2.95
Left IFG	-48	28	12	3.51
Left caudate nucleus	-32	18	0	2.57
Left cingulate gyrus	-12	4	30	2.57
Left STG	-54	-12	-6	3.28
Left pMTG	-44	-56	6	4.11
Left fusiform gyrus	-20	-72	-6	4.23
Vermis	-8	-60	-26	3.15
Right ATL	36	10	-26	3.85
Right lingual gyrus	22	-80	-5	3
Right STG	60	-4	-8	3.21
Right ITG	52	62	-12	3.41

288  
 289 *ITG = inferior temporal gyrus, pMTG = posterior middle temporal gyrus, IFG = inferior frontal gyrus.*

290 *Significant at  $p < 0.05$  corr. over SVC. All coordinates refer to MNI space.*

291  
 292 Importantly, within-block adaptation specific to semantic categories versus others did not yield any  
 293 activity in the regions involved in semantic control (e.g., IFG and pMTG), supporting the fact that these  
 294 latter regions are not involved in semantic representation itself nor in thematic associations but play  
 295 a more general and less category-specific role in the context of our task.  
 296 Moreover, note that in order to further demonstrate that within-block signal changes were related to  
 297 semantic processing and not to mere effect of time or item repetition (Kalm and Norris 2017),  
 298 responses to ‘pseudo-blocks’ straddling from the end of a semantic category to the beginning of

299 another (e.g., items 5-6-7 of “colours” family and 1-2-3 of “animals”) had also been assessed. This  
 300 analysis did not yield any significant response (whole brain thresholded at  $p < 0.001$  uncorrected).

301

302 **Table 4.** *Semantic-related adaptation activations throughout scanning session, regardless of specific*  
 303 *semantic category.*

304

Area	MNI coordinates			z score
	x	y	z	
Left IFG	-46	28	12	3.22
Left ITG	-54	-38	-6	2.68
Left pMTG	-54	-52	2	3.40
Left fusiform gyrus	-21	-70	-5	3.29
Left angular gyrus	-28	-68	22	3.57
Right IFG	36	48	-14	3.24
Right anterior cingulate gyrus	2	32	22	2.79
Right pMTG	54	-38	-6	3.01

*ITG = inferior temporal gyrus, pMTG = posterior middle temporal gyrus, IFG = inferior frontal gyrus, ITG = inferior temporal gyrus.*

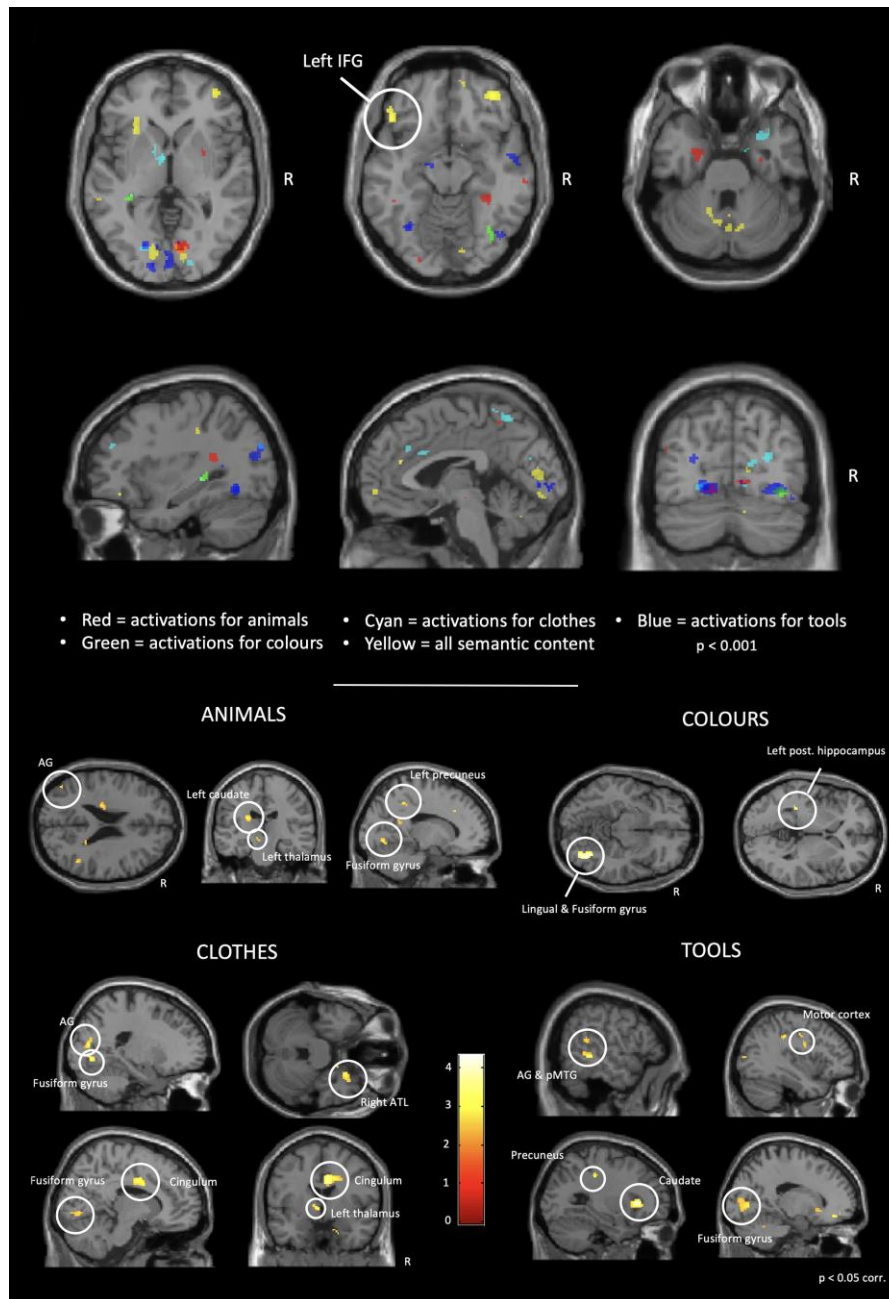
*Significant at  $p < 0.05$  corr. over SVC. All coordinates refer to MNI space.*

305

306 We also ran a mixed ANOVA on BOLD signal ( $\beta$  values of category-specific contrasts, i.e., ‘tools vs all’)  
 307 to directly test the interaction between repetition and brain region (ROIs). We observed the following  
 308 results: tools, left IFG vs fusiform gyrus\* - interaction:  $p = 0.0028$ ; clothes, left IFG vs right ATL\*\* -  
 309 interaction:  $p = 0.0034$ ; animals, left IFG vs precuneus\*\*\* - interaction:  $p = 0.001$ ; colour names  
 310 repetition, left IFG vs right fusiform\*\*\*\* - interaction,  $p = 0.0041$  (IFG at [-46, 28, 12], \* fusiform gyrus  
 311 at [-20, -74, -4]; \*\*right ATL at [30, 14, -34]; \*\*\*right precuneus at [-10, -40, 40]; \*\*\*\* right fusiform at  
 312 [8, -80, -2]). This additional analysis confirms our initial observation of a null response for category-  
 313 specific semantic adaptation in control regions in comparison with representational areas.

314 **Figure 3.** Within-semantic block activations related to specific semantic categories.

315



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318

*The results are shown at a statistical of  $p < 0.001$  uncorrected, or  $p < 0.05$  FWE corrected over SVC.*

319

320 Finally, to further understand the dynamics of semantic control, a psychophysiological interaction (PPI)

321 analysis was conducted for each semantic family in order to determine to which extent the category-

322 specific processing regions and the semantic control network are functionally connected to each other

323 in each block. We chose the left IFG as seed region because of the high reliability of its involvement

324 across numerous studies regarding semantic control that surpass that of pMTG (Jefferies 2013; Ralph

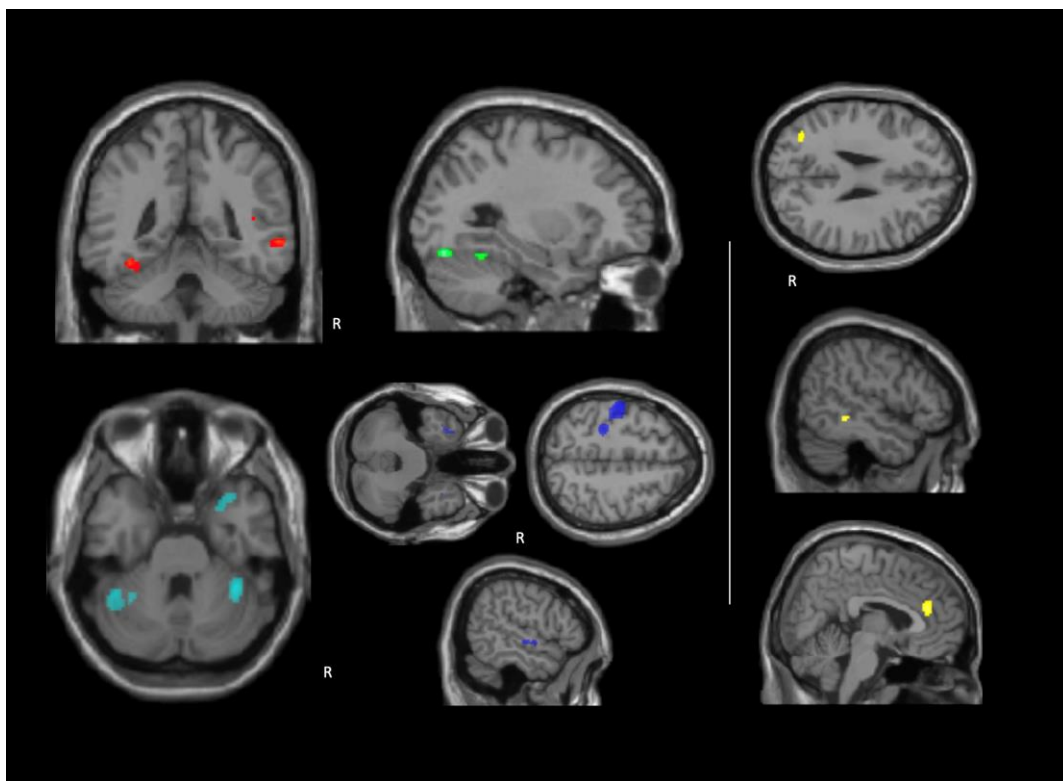


325 et al. 2016b; Chiou et al. 2018; Jefferies et al. 2020). As shown in Table 5, we found significant  
 326 functional connectivity between the IFG seed region and the other regions involved in the  
 327 representation of semantic information that had already been highlighted for the category-specific  
 328 contrasts in the preceding analyses (see Figure 4).

329

330 **Figure 4.** PPI results. Main cerebral regions that functionally connect to left IFG during covert  
 331 presentation of stimuli from specific semantic categories (left) and for all semantic stimuli (right).

332



333

334

335 *Functional connectivity results: for animal names (red), for colors (green blobs), for clothes names (cyan) and for tool names (blue blobs).*

336 *Functional connectivity for all semantic stimuli is presented on the right, with yellow blobs. Results are displayed at a statistical threshold of*

337  *$p < 0.001$  uncorrected.*

338

339 For tool names, left IFG activity was correlated to left motor cortex, left (anterior) STG, left angular  
 340 gyrus and left ATL. For animal names the latter correlated with left fusiform gyrus, left hippocampus  
 341 and right precuneus. For colours we found significant association with right fusiform gyrus, left

342 posterior hippocampus and right hippocampus. For clothes, left IFG activity correlated with left  
 343 precuneus, right middle cingulate gyrus and right ATL.

344 Ultimately, we conducted a PPI analysis over all semantic categories at the same time, in order to  
 345 highlight also functional connectivity with the left pMTG: if the semantic control network is involved  
 346 in a domain-general manner during semantic adaptation, the functional connectivity between the left  
 347 IFG seed region and the pMTG should be observed when assessing connectivity independently of type  
 348 of semantic category. When running this analysis, (see Table 5 and figure 4), we indeed observed  
 349 significant functional connectivity between the left IFG and the left pMTG, as well as the right IFG and  
 350 anterior cingulate cortex involved in semantic control or more general executive control.

351

352 **Table 5.** PPI results. First panel shows cerebral regions correlating with BOLD response in the left IFG  
 353 during passive listening of specific semantic families versus all others. Second panel lists regions that  
 354 correlate with left IFG for all semantic content.

355

	<i>MNI coordinates</i>			<b>z score</b>
	<b>x</b>	<b>z</b>	<b>z</b>	
<b>TOOLS</b>				
Left motor cortex	-54	-44	46	3.84
Left STG	-40	-4	-16	4.73
Left angular gyrus	-42	-60	26	3.75
Left ATL	-30	16	-34	3.92
<b>ANIMALS</b>				
Left fusiform gyrus	-20	-78	-16	5.67
Left hippocampus	-28	4	-18	5.09
Right precuneus	12	-36	44	4.88
<b>COLOURS</b>				
Right fusiform gyrus	17	-80	-11	3.92
Left post. hippocampus	-34	-36	2	3.17
Right hippocampus	38	-30	-20	3.71
<b>CLOTHES</b>				
Left precuneus	-2	-12	76	4.04
Right mid. cingulate gyrus	12	6	38	3.84
Right ATL	33	12	-30	3.45
<b>ALL SEMANTIC</b>				
	<i>MNI coordinates</i>			
	<b>x</b>	<b>z</b>	<b>z</b>	<b>z score</b>

Left pMTG	-44	-56	-8	3.97
Left ant. cingulate gyrus	-2	38	22	2.56
Left angular gyrus	-32	-70	30	2.53
Right IFG	46	40	-18	2.64

*STG = superior temporal gyrus, ATL = anterior temporal lobe, pMTG = posterior middle temporal gyrus, IFG = inferior frontal gyrus.*

*Significant at  $p < 0.05$  corr. over SVC (10 mm radius). All coordinates refer to MNI space.*

356

357

## 358 Discussion

359 This study examined the nature of the semantic control network by assessing its involvement in  
 360 implicit semantic processing tasks. Using an fMRI adaptation paradigm for incidentally activated  
 361 semantic information we observed robust adaptation within the ATL, the AG and ventral temporo-  
 362 occipital areas across all semantic categories, consistent with implicit activation of semantic  
 363 knowledge. These regions also showed semantic category-specific differences in neural responses.  
 364 Most importantly, adaption was observed across all categories, without any category-specific  
 365 differences, in the IFG and pMTG associated with semantic control. This was observed while  
 366 participants could not direct their attention to the stimuli nor process semantic information in any  
 367 explicit and controlled manner. The implicit nature of these semantic and semantic control responses  
 368 is further supported by the high hit rate for the demanding visual search task and the participants'  
 369 debriefing reports, showing that participants were unable to recall or recognize most of the  
 370 presented words and that they were unaware of the organization of the words into semantically  
 371 coherent blocks.

372 The activity of the pMTG in covert semantic processing here is important to be highlighted given that  
 373 it had been specifically associated with explicit, judgement-based and demanding semantic tasks in  
 374 previous studies (Davey et al. 2016; Thompson et al. 2016; Jefferies et al. 2020), for instance when  
 375 ongoing retrieval needs to be shaped to context (e.g., in a task where the association honey >  
 376 marriage would prevail over honey > bee). Our results suggest that, under conditions promoting  
 377 automatic semantic processing, semantic control areas can nevertheless be recruited, potentially  
 378 following a bottom-up information transfer from semantic representation-specific regions.

379 The CSC framework would anticipate recruitment of pMTG and IFG when activation within the  
380 semantic system itself triggers the engagement of control (e.g. ambiguous or unexpected inputs)  
381 (Jefferies 2013; Ralph et al. 2016a). Our data suggest that this recruitment also occurs in the absence  
382 of conscious semantic processing.

383 The finding of semantic control network recruitment in covert conditions could indicate that this  
384 network is not specific to explicit or conscious semantic control. It could be argued that semantic  
385 control network activation in covert semantic processing conditions is a mere bottom-up activation  
386 resulting from connections between the transmodal hubs (ATL) and the semantic control network  
387 (Binney et al. 2012; Ralph et al. 2016b). It is important to note here that our PPI analysis showed  
388 highly specific functional connectivity patterns between the frontal part of the semantic control  
389 network and specific semantic processing areas indicating that the control network is not just  
390 generally co-activated in covert semantic processing. Rather, it adapts its functional connectivity to  
391 category-specific semantic processing areas, as a function of the specific semantic features being  
392 (covertly) processed. The intervention of the semantic control network in a covert semantic  
393 habituation paradigm as used in this study may reflect the progressive diminution of covert semantic  
394 monitoring processes, as the semantic control network gradually detects the predictability and the  
395 within-block semantic coherence of presented words.

396 Confusions between everyday objects when simultaneously available (such as between a fork and a  
397 spoon) or difficulties in retrieving the use of objects when no contextual cues are available (Jefferies  
398 and Lambon Ralph 2006; Ralph et al. 2016b; Jackson et al. 2021) as observed in patients with  
399 semantic aphasia (SA) may be the consequence of the degradation of 'automatic' semantic control.

400 Naming or verbal fluency impairment in these patients may also stem at least partially from these  
401 control deficits. The poor capacity of SA patients to perceive subtle contextual aspects in a  
402 conversation, such as homonym discrimination, implied meaning or even humor (Jefferies and  
403 Lambon Ralph 2006; Hoffman et al. 2018), may be further aspects linked to automatic semantic  
404 control impairment. Unlike in patients with semantic dementia, cueing often allows patients with SA

405 to perform better in various semantic tasks, clearly showing that at least some of their difficulties are  
406 related to loss of control and retrieval mechanisms rather than a loss of semantic knowledge  
407 (Chapman et al. 2020).

408 Given the domain-general aspects of semantic control (Hoffman et al. 2009; Jackson et al. 2021), we  
409 should indeed expect the same ‘automatic control’ mechanisms to apply for verbal and other  
410 modalities such as visual, non-verbal auditory, olfactive or tactile stimuli. The fMRI adaptation  
411 paradigm presented in this study could indeed be easily extended to other stimuli, by presenting  
412 streams of non-verbal auditory stimuli sharing or not semantic features. However, when using  
413 streams of visual objects, the main task on which the focus of attention is directed would need to be  
414 changed as there would be interference between the visual nature of the main task and the  
415 incidentally attended stream of visual objects.

416 As mentioned above, AG is a complex region, and its precise functions are still a matter of debate  
417 (Seghier et al. 2010). The strong AG response we observed for both general semantic and category-  
418 specific adaptation reflects this complexity, indicating that the AG and its different subparts may  
419 subserve both specific semantic and more general control processes.

420 Finally, our results can also be considered in the light of recent computational models of the  
421 semantic system which have integrated control and representational mechanisms (Hoffman et al.  
422 2018; Jackson et al. 2021), unifying the Hub-and-Spoke theory (Ralph et al. 2016b) and the Controlled  
423 Semantic Cognition Framework (Ralph et al. 2016b; Jefferies et al. 2020). These models also allow for  
424 dynamic properties such as recent experience buffering and conceptual learning, as well as damage  
425 caused by degeneration or stroke. The reverse-engineered model developed by Jackson et al. posits  
426 that semantic cognition relies on indirect interactions between a single deep multimodal hub  
427 (putatively the ATL) and modality-specific representational areas (spokes). Regarding control  
428 mechanisms, simulations provided significantly better results when control operated on the  
429 modality-specific areas than on its deep components (Jackson et al. 2021). This model therefore  
430 predicts that control regions should not directly connect to ATL. The present study supports this

431 prediction, as we did not observe any significant functional connectivity between the IFG and ATL  
432 ROIs, but significant connectivity between the IFG and other category-specific representational  
433 areas. Moreover, Hoffman et al. proposed a computational model combining a Hub-and-spokes  
434 architecture with a ‘buffer’ system that allows activated semantic information to be influenced by  
435 current context; this interaction between semantic knowledge and context has been proposed to be  
436 supported by the ventral parietal cortex (VPC). The strong and persistent neural responses we  
437 observed in ventro-parietal cortex (AG) may support this prediction as the AG response pattern  
438 differed from the other semantic ROIs in that it was neither specific to semantic knowledge nor to  
439 control.

440

## 441 **Conclusions**

442 Automatic semantic processing of an unattended verbal stream recruits not only posterior cortices  
443 known as unimodal and amodal semantic representation areas, but also IFG and pMTG, which are  
444 usually associated with semantic control. Moreover, the left IFG showed category specific functional  
445 connectivity with different semantic processing areas in temporal cortices and brain regions  
446 associated. These results indicate that semantic control processes do not only intervene in explicit,  
447 judgment based semantic tasks but also in implicit semantic processing tasks. The fronto-temporal  
448 semantic control network may be involved in the covert detection of semantic regularities allowing  
449 for more efficient identification and selection of semantic representations in temporal cortices.

450

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455

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