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Incidental Verbal Semantic Processing Recruits the Fronto-temporal Semantic Control Network

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Abstract

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

Key words: IFG, incidental, pMTG, repetition suppression, semantic control

Introduction

Semantic cognition refers to a range of cognitive processes and representations encoded in distributed brain areas (Binder et al. 2009; Price 2012) that define our knowledge of objects, word meanings, facts and people (Ralph et al. 2016a). An influential model, the controlled semantic cognition (CSC) framework (Ralph et al. 2016a; Chiou et al. 2018; Thompson et al. 2018; Jefferies et al. 2020), posits that semantic cognition relies on the interaction between semantic representations on the one hand, and their control on the other (Ralph et al. 2016a). Semantic knowledge involves specific, low-level as well as generalizable high-level, relationships between sensory, motor, linguistic and affective features as well as their integration. Semantic control allows the manipulation of these representations and to

generate context-specific semantic inferences based on interactions between modality-specific sources of information (Lambon Ralph et al. 2010b).

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

The “semantic control” system relies primarily on the inferior frontal gyrus (IFG) and the posterior middle temporal gyrus (pMTG) (Thompson-Schill et al. 1999; Badre and Wagner 2005; Rodd et al. 2005; Jefferies and Lambon Ralph 2006; Binder et al. 2009; Noonan et al. 2010; Seghier et al. 2010; Davey et al. 2016; Jefferies et al. 2020). This system is thought to monitor and modulate the activity of semantic knowledge areas (Devlin et al. 2003; Yarkoni et al. 2011; Huang et al. 2012; Jefferies 2013; Zhu et al. 2013; Della Rosa et al. 2018) and may adapt itself when one or more of the CSC components are compromised by damage, with IFG and pMTG being able to mutually compensate for their failure, or in case of demanding tasks (Jefferies 2013; Davey et al. 2015; Ralph et al. 2016a; Hallam et al. 2018; Jefferies et al. 2020).

Neural substrates of both unimodal and multimodal semantic representations have been shown to be recruited by preconscious stimuli, suggesting that semantic knowledge can be processed under conditions of reduced or even absent awareness (Perrin et al. 2002; Gaillard et al. 2006; Kouider and Dehaene 2007). By contrast, semantic control is generally believed to rely on conscious processes and is generally assessed by tasks involving explicit judgment and decision making processes (Ralph et al. 2016; Jefferies et al. 2020) although the amount of semantic control has sometimes been manipulated in a less explicit manner (Badre and Wagner 2002). Some authors have also considered the theoretical possibility of automatic control process (Badre and Wagner 2005; Davey et al. 2015). These control processes, supported by the IFG, are further believed to exert a top-down influence onto unimodal semantic representation areas (Chiou et al. 2018). However, the possibility remains that semantic control processes may also be at least partially independent of explicit control processes. Indeed patients with semantic control deficits can show increased effects of semantic interference and intrusion errors when no explicit semantic judgment is required: when repeatedly naming pictures from the same versus a different semantic category, these patients show increased semantic interference effect relative to healthy controls (Schnur et al. 2006; Hamilton and Martin 2007). It could however be argued that this task, although not directly involving explicit semantic control in the form of semantic judgment, may however be considered as an explicit task as the participants have to produce a target response in a top-down manner. Currently, we do not know whether the semantic control network involves purely explicit semantic control processes or whether it can also be recruited incidentally.

We addressed this question by assessing brain responses to semantic information using an incidental semantic activation paradigm. Regional brain responses to the semantic attributes of an unattended auditory word stream were recorded while the participants’ attentional control was monopolized by a demanding visual search task in which participants had to detect an open circle among full circles and then indicate the location of the aperture (see Fig. 1). This task is considered to demand a high degree of visual selective attention, decision making, and motor control (Davis and Palmer 2004; Ettenhofer et al. 2016; Schill et al. 2020). Neural sensitivity to semantic processing was assessed using a functional magnetic resonance imaging (fMRI) response adaptation paradigm (also known as repetition suppression) (Grill-Spector 2006; Garrido et al. 2009; Larsson and Smith 2012). This phenomenon refers to the reduction of local brain responses to repeated presentation of a specific stimulus type or attribute (Grill-Spector and Malach 2001; Sayres and Grill-Spector 2006). Representational areas have been shown to present such a repetition adaptation of neural responses during

same semantic family word presentation (Chouinard et al. 2008; Yee et al. 2010; Menenti et al. 2012). In this study, we aimed to determine whether response adaptation in semantic representational areas would also be obtained by purely incidental semantic stimulation, when no semantic information is processed in a conscious and voluntary manner. Here, while the participants were carrying out the visual search task, auditory blocks of 5 to 7 words from the same semantic category (tools, clothes, colors, or animals) were presented (see Fig. 1). We reasoned that brain areas sensitive to semantic processing of the word stream would decrease their response during the presentation of a given homogenous semantic block and increase again at the beginning of the following block.

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

Materials and Methods

Participants

A total of 14 healthy right-handed volunteers (age range 18–26 y., 8 females) gave their written informed consent to participate in this study and received a financial compensation. They were nonsmokers, native French-speakers, had normal audition and normal or corrected-to-normal vision. They had not any history of medical, neurological or psychiatric disorders. The study was approved by the Ethics Committee of the Faculty of Medicine of the University of Liège.

Experimental Design

Participants were told that they participated in an fMRI study focusing on visual attention, which implied performing a demanding visual search task in a noisy environment (Fig. 1). In this task, each trial consisted of the 1500 ms display of 15 to 20 randomly distributed circles (2-cm diameter, distributed over a 20 × 20 area). All of them were complete except one that was open by 6.2° at random angle. Participants were instructed to specify whether the circle opening was left or right-handed. When the opening was at the top or the bottom of the circle, the opening side was left free to decide by participants. Simultaneously, verbal stimuli, presented as distractors, were delivered through headphones. Frequent, concrete, imageable, and unambiguous French words, 1 to 3-syllable long, were selected based on their frequency of occurrence in the usual oral language (>500 of literal frequency, as assessed by BRULEX index (Pagel et al. 1998), from four semantic categories (tools, clothes, colors, and animals). Homophone and polysemic words were discarded (see Table 1).

The words were prerecorded by a male speaker and presented in blocks of five to seven words from the same semantic category, at the rate of one word every 2000 ms. Each word was presented several times, with an equal probability to occur in any position within the semantic block. The block themselves were presented in a random order. Each run lasted 3 to 5 min

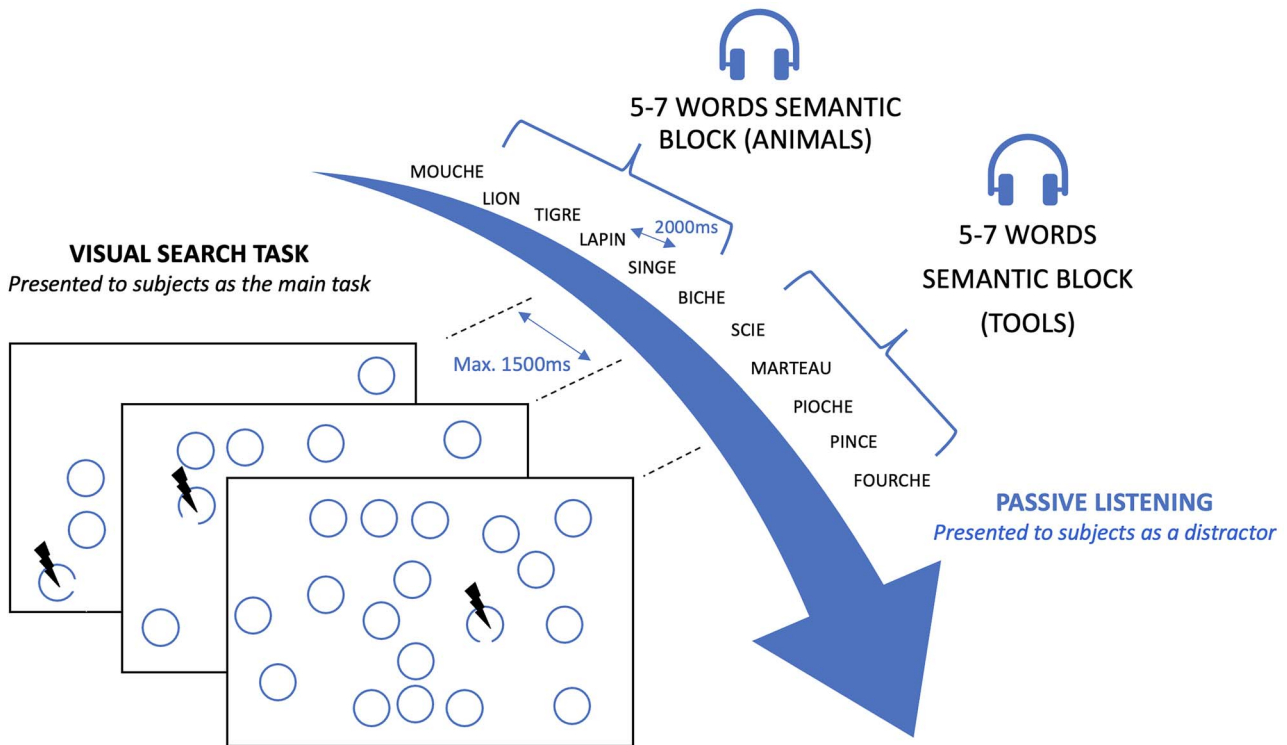


Figure 1. Schematic representation of experimental design.

Table 1 Presented words by semantic family (in French)

| Tools | Clothes | Colors | Animals |
|---------|----------|--------|----------|
| 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 |

according to the number of presented words and three runs were repeated in a row within the MR scanner, with interleaved 3- to 5-min resting periods (see Fig. 1).

After the MRI sessions, participants were debriefed using questionnaires successively probing their feelings about the visual task and their feedback, then assessing their comfort and their perception of the “background noise,” the words that they heard, the words that they were able to remember and finally, whether they identified any structure in the word stream. This assessment was meant to exclude subjects who may have had an explicit identification of the semantic nature of the stimuli as they may not have focused exclusively on the visual search task. A debriefing questionnaire further assessed of the covert nature of the stimuli and the level of attention paid by participants to the auditory material as well as to the visual display (see Results for further information).

Recordings

Data were acquired with a 3 T head-only magnetic resonance (MR) scanner (Siemens MAGNETOM Allegra) using a

gradient echo-planar sequence [Gradient echo-planar (EPI) axial slice orientation whole brain/most of the brain, 34 slices, FoV=192 × 192 mm², voxel size 3 × 3 × 3 mm³, 25% interslice gap, matrix size 64 × 64 × 34, TR=2040 ms, TE=30 ms, Flip Angle=90°]. In all sessions, the first three volumes were discarded to account for magnetic saturation effects on brain tissue. A structural MR scan was acquired at the end of the experimental session (T1-weighted three-dimensional magnetization-prepared rapid-acquisition gradient echo sequence; TR, 1960 ms; TE, 4.43 ms; inversion time, 1100 ms; FOV, 230 × 173 mm²; matrix size, 256 × 192 × 176; voxel size, 0.9 × 0.9 × 0.9 mm). Stimuli were displayed using a video projector on a screen positioned at the rear of the scanner, which the subject could comfortably see through a mirror mounted on the standard head coil. The responses of the subjects to the distracting visual task were recorded using a small MRI compatible keyboard.

Data Analysis

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

The analysis conformed to a mixed effects analysis and accounted for fixed and random effects (RFX). For each subject, a general linear model was used to estimate brain responses at

each voxel. Trials corresponding to events of the four semantic categories (tools, clothes, colors, and animals) as well as events of the visual search task were modeled as stick functions and convolved with the canonical hemodynamic response function.

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

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

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

Summary statistics images were smoothed (Gaussian kernel, 6 mm FWHM) and entered in the RFX analysis. Statistical inferences were performed at the cluster level at $P < 0.05$, with family-wise error (FWE) corrections for multiple comparisons across the entire brain volume, with a cluster-forming threshold of $P < 0.001$ uncorrected; this procedure has been shown to minimize the likelihood of false positives (Eklund et al. 2016). For the region of interest (ROI) analyses, the threshold was also defined at $P < 0.05$ with small volume FWE corrections based on Gaussian random field theory over small spherical volumes (10-mm radius) located in structures of interest reported in the literature focusing on semantic processing and semantic cognition. These ROI were defined based on the average coordinates published in the literature and involving the angular gyrus (AG) (Seghier et al. 2010), the temporal poles, the lingual and fusiform gyri (Dehaene et al. 2002; Jefferies and Lambon Ralph 2006; Ruff et al. 2008; Binney et al. 2010; Price 2010a; Seghier and Price 2012; Ulrich et al. 2015; Teige et al. 2018). We further considered the anterior superior temporal gyrus (STG) as this part has also been associated with access to semantic knowledge (Ruff et al. 2008; Visser and Lambon Ralph 2011; Rämä et al. 2012; Hallam et al. 2018). For the semantic control framework, ROIs involved the IFG and pMTG based on the spatial coordinates published by Jefferies et al. and Badre. A priori locations of interest were the following: AG [−47, −59, 25] (Price 2010a) and [−30, −64, 24] (Seghier et al. 2010; Price 2010a; Seghier and Price 2012; Price et al. 2015), ATL [−38, 18, −24] (Damasio et al. 2004; Visser et al. 2012; Rice et al. 2015), right ATL [40, 24, −33] (Price 2010; Visser et al. 2012), fusiform gyrus [−30, −70, −10] (Dehaene et al. 2002; Jefferies and Lambon Ralph 2006; Ruff et al. 2008; Binney et al. 2010; Price 2010a; Seghier and Price 2012; Ulrich et al. 2015; Teige et al. 2018), STG [−46, −6, −10] (Ruff et al. 2008; Visser and Lambon Ralph 2011; Rämä et al. 2012; Hallam et al. 2018), IFG [−54, 18, 8] and pMTG [−56, −50, 3] (Badre et al. 2005; Whitney et al. 2011; Teige et al. 2018). Stereotactic coordinates refer to the MNI space.

We also investigated functional connectivity between activity in the left IFG and distant brain regions involved in semantic processing. Using psychophysiological interaction (PPI, Friston et al. 1997; Gitelman et al. 2003) we determined to which extent

category-specific processing regions interacted with the semantic control network.

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

Results

Behavioral Results

All subjects performed the task with relatively high accuracy (mean $72.4 \pm 8\%$ hits), suggesting that participants focused on the visual task as instructed. At debriefing, none was aware that words were organized by semantic categories although most participants could recall a few words (5.61 ± 1.06 words, out of 28). Participants also reported strong engagement in the visual search task as they described their behavior as “focused” to “very focused” for this task. Participants described the visual task as “demanding” to “very difficult”, and the background noise as “not bothering” to “slightly bothering”. Most of them appeared to have been more disturbed by the MRI noise itself. They were unable to reliably identify presented words among other words in a list (mean identification: 6.12 ± 1.9 out of 28 target words presented together with non-target words in a complete list of 40 words). Finally, when asked to cite five animal, tool or clothes names, subjects produced very few words that had been presented during the experimental task in the scanner. For clothes an average of 1.2 ± 0.5 names were identical to one of presented words; for animals, this number was 1.1 ± 0.4 identical and for tools it was 0.8 ± 0.3 . Color words were not assessed given the limited number of color words that can be produced.

Functional MRI Results

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

the semantic representation amodal network (see Table 4 and Fig. 2).

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

Selective within-block adaptation to cloth names (versus all others) was significant in left AG, left thalamus, right middle cingulate gyrus, and right ATL (Table 2, Fig. 3). Overall, these results show that semantic processing areas were selectively and automatically recruited by covert auditory stimuli in the same way they transmodally encode conceptual representations of concrete objects and their properties in overt studies (Thompson-Schill 2003; Wheatley et al. 2005; Barsalou 2008; Kiefer and Pulvermüller 2012) with a differentiation of a dorsal stream (involved in the representations of semantics related to movements and actions and a ventral stream (involved in the semantic representation of shapes and color (Bartels and Zeki 2000; Hubbard et al. 2011; Perlman et al. 2011; Weiner and Zilles 2016; Neudorf et al. 2019), and a more general involvement of left

Table 2 Within-semantic block adaptation—Specific semantic categories

| | MNI coordinates | | | z Score |
|----------------------------|-----------------|-----|-----|---------|
| | x | y | z | |
| Tools | | | | |
| 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 |
| Animals | | | | |
| 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 |
| Colors | | | | |
| 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 |
| Clothes | | | | |
| 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 |

Note: ITG = inferior temporal gyrus, STG = superior temporal gyrus, pMTG = posterior middle temporal gyrus, ATL = anterior temporal lobe. Significant at $P < 0.05$ corr. over small volume correction (SVC). All coordinates refer to MNI space.

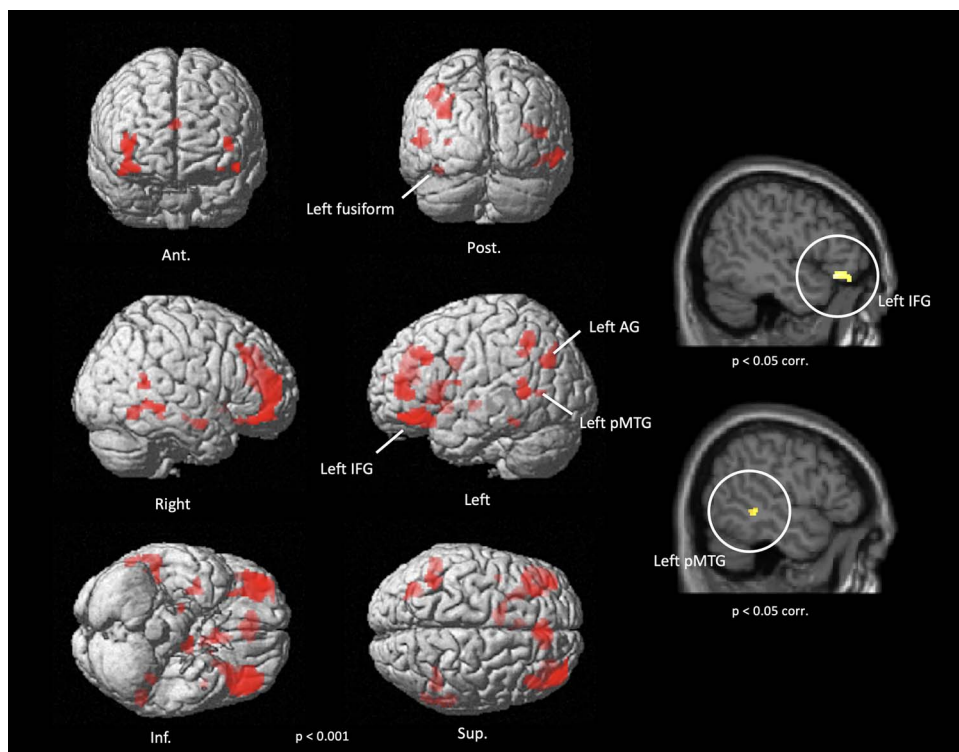


Figure 2. Semantic-related adaptation activations throughout scanning session—all semantic categories included. The results are shown at a statistical of $P < 0.001$ uncorrected, or $P < 0.05$ family-wise error (FWE) corrected over small volume correction (SVW).

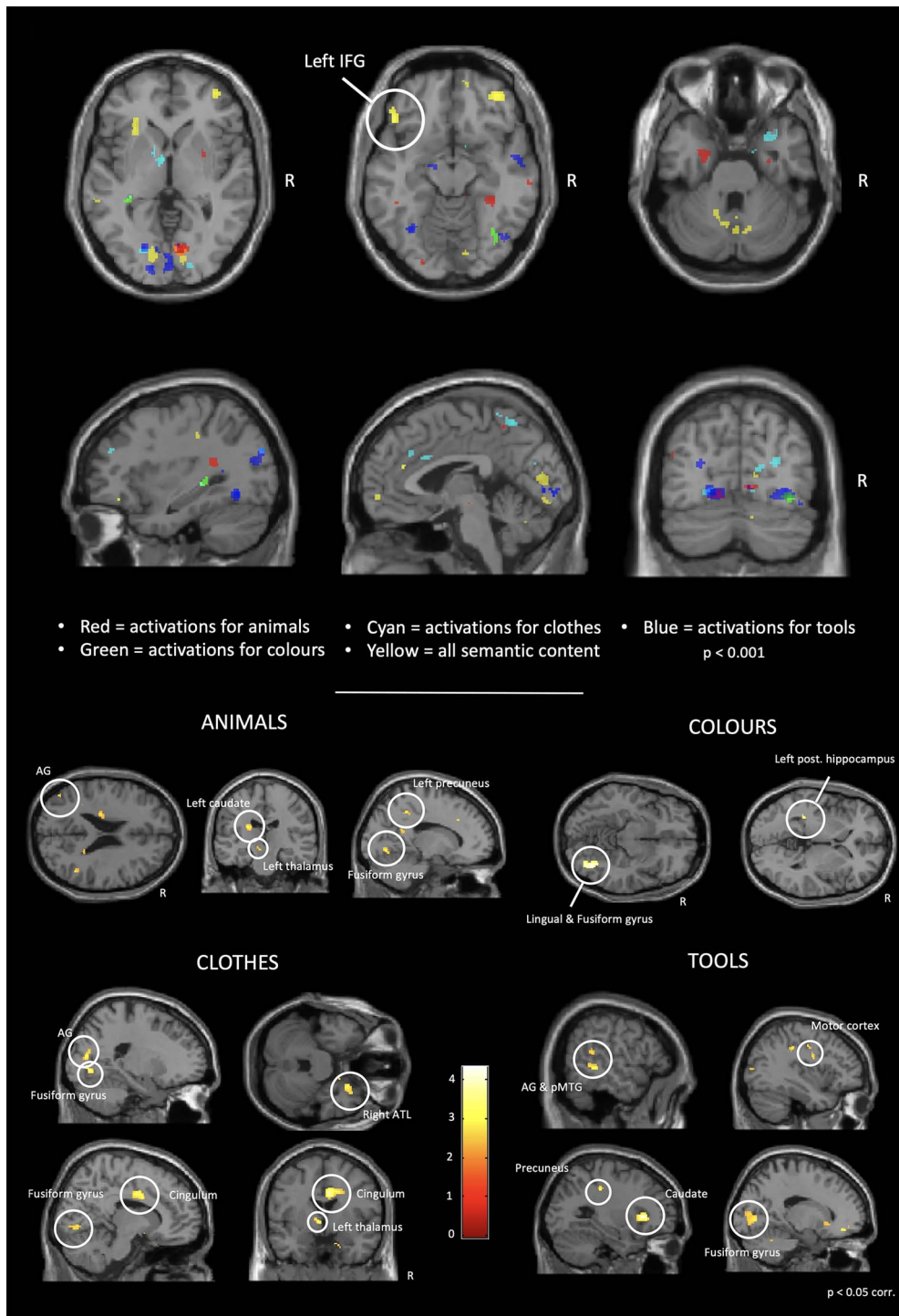


Figure 3. Within-semantic block activations related to specific semantic categories. The results are shown at a statistical of $P < 0.001$ uncorrected or $P < 0.05$ family-wise error (FWE) corrected over small volume correction (SVW).

AG which has been regarded as a thematic hub for semantic representation (Lewis et al. 2019) as well as essential for automatic retrieval of specific semantic information (Davey et al. 2015; Jefferies et al. 2020) or more recently as a multimodal “automatic” buffer (Humphreys et al. 2015; Humphreys and Lambon Ralph 2015).

Importantly, within-block adaptation specific to semantic categories versus others did not yield any activity in the regions involved in semantic control (e.g., IFG and pMTG), supporting the fact that these latter regions are not involved in semantic representation itself nor in thematic associations but play a more general and less category-specific role in the context of our task.

Table 3 Within-semantic block adaptation—All semantic categories included

| 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 |

Note: ITG = inferior temporal gyrus, pMTG = posterior middle temporal gyrus, IFG = inferior frontal gyrus. Significant at $P < 0.05$ corr. over SVC. All coordinates refer to MNI space.

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

| 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 |

Note: 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.

Moreover, note that in order to further demonstrate that within-block signal changes were related to semantic processing and not to mere effect of time or item repetition (Kalm and Norris 2017), responses to “pseudo-blocks” straddling from the end of a semantic category to the beginning of another (e.g., items 5–6–7 of “colors” family and 1–2–3 of “animals”) had also been assessed. This analysis did not yield any significant response (whole brain thresholded at $P < 0.001$ uncorrected).

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

Table 5 PPI results; the first panel shows cerebral regions correlating with BOLD response in the left IFG during passive listening of specific semantic families versus all others; the second panel lists regions that correlate with left IFG for all semantic content

| | MNI coordinates | | | z Score |
|----------------------------|-----------------|-----------------|-----|---------|
| | x | z | z | |
| Tools | | | | |
| 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 |
| Animals | | | | |
| Left fusiform gyrus | -20 | -78 | -16 | 5.67 |
| Left hippocampus | -28 | 4 | -18 | 5.09 |
| Right precuneus | 12 | -36 | 44 | 4.88 |
| Colors | | | | |
| Right fusiform gyrus | 17 | -80 | -11 | 3.92 |
| Left post. Hippocampus | -34 | -36 | 2 | 3.17 |
| Right hippocampus | 38 | -30 | -20 | 3.71 |
| Clothes | | | | |
| Left precuneus | -2 | -12 | 76 | 4.04 |
| Right mid. Cingulate gyrus | 12 | 6 | 38 | 3.84 |
| Right ATL | 33 | 12 | -30 | 3.45 |
| | | MNI coordinates | | z Score |
| | | x | z | |
| All Semantic | | | | |
| 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 |

Note: 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.

Finally, to further understand the dynamics of semantic control, a PPI analysis was conducted for each semantic family in order to determine to which extent the category-specific processing regions and the semantic control network are functionally connected to each other in each block. We chose the left IFG as seed region because of the high reliability of its involvement across numerous studies regarding semantic control that surpass that of pMTG (Jefferies 2013; Ralph et al. 2016b; Chiou et al. 2018; Jefferies et al. 2020). As shown in Table 5, we found significant functional connectivity between the IFG seed region and the other regions involved in the representation of semantic information that had already been highlighted for the category-specific contrasts in the preceding analyses (see Fig. 4).

For tool names, left IFG activity was correlated to left motor cortex, left (anterior) STG, left angular gyrus and left ATL. For animal names the latter correlated with left fusiform gyrus, left hippocampus and right precuneus. For colors we found significant association with right fusiform gyrus, left posterior hippocampus and right hippocampus. For clothes, left IFG activity correlated with left precuneus, right middle cingulate gyrus and right ATL.

Ultimately, we conducted a PPI analysis over all semantic categories at the same time, in order to highlight also functional

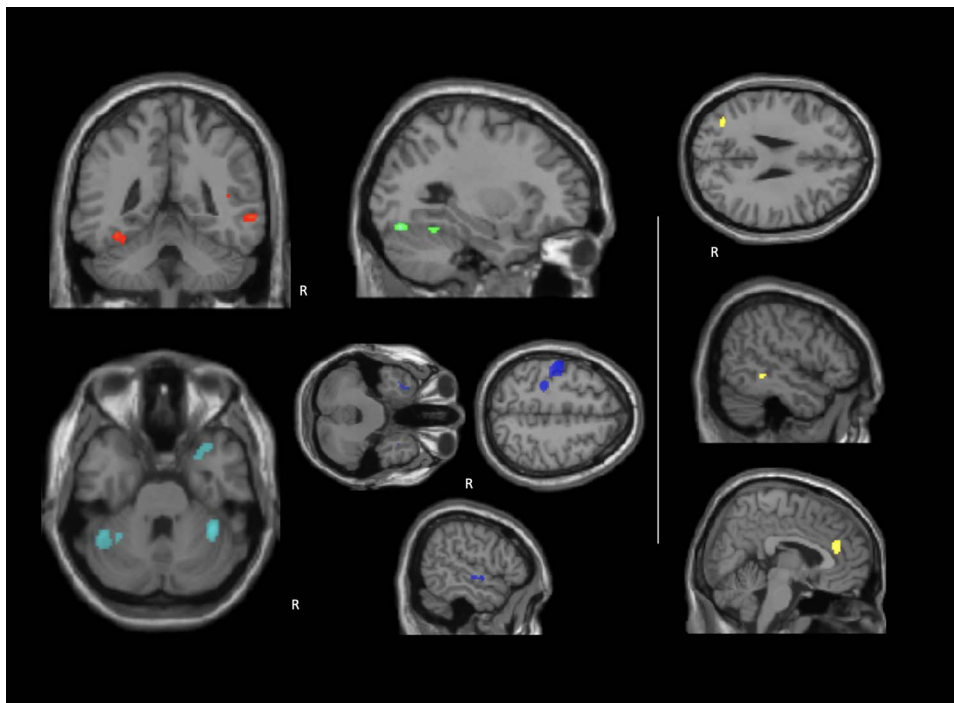


Figure 4. PPI results. Main cerebral regions that functionally connect to left IFG during covert presentation of stimuli from specific semantic categories (left) and for all semantic stimuli (right). Functional connectivity results: for animal names (red), for colors (green blobs), for clothes names (cyan), and for tool names (blue blobs). Functional connectivity for all semantic stimuli is presented on the right, with yellow blobs. Results are displayed at a statistical threshold of $P < 0.001$ uncorrected.

connectivity with the left pMTG: if the semantic control network is involved in a domain-general manner during semantic adaptation, the functional connectivity between the left IFG seed region and the pMTG should be observed when assessing connectivity independently of type of semantic category. When running this analysis, (see Table 5 and Fig. 4), we indeed observed significant functional connectivity between the left IFG and the left pMTG, as well as the right IFG and anterior cingulate cortex involved in semantic control or more general executive control.

Discussion

This study examined the nature of the semantic control network by assessing its involvement in implicit semantic processing tasks. Using an fMRI adaptation paradigm for incidentally activated semantic information we observed robust adaptation within the ATL, the AG, and ventral temporo-occipital areas across all semantic categories, consistent with implicit activation of semantic knowledge. These regions also showed semantic category-specific differences in neural responses.

Most importantly, adaption was observed across all categories, without any category-specific differences, in the IFG and pMTG associated with semantic control. This was observed while participants could not direct their attention to the stimuli nor process semantic information in any explicit and controlled manner. The implicit nature of these semantic and semantic control responses is further supported by the high hit rate for the demanding visual search task and the participants' debriefing reports, showing that participants were unable to recall or recognize most of the presented words and that they were unaware of the organization of the words into semantically coherent blocks.

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

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

The finding of semantic control network recruitment in covert conditions could indicate that this network is not specific to explicit or conscious semantic control. It could be argued that semantic control network activation in covert semantic processing conditions is a mere bottom-up activation resulting from connections between the transmodal hubs (ATL) and the semantic control network (Binney et al. 2012; Ralph et al. 2016b). It is important to note here that our PPI analysis showed highly specific functional connectivity patterns between the frontal part of the semantic control network and specific semantic processing areas indicating that the control network is not just generally co-activated in covert semantic processing. Rather, it adapts its functional connectivity to category-specific semantic processing areas, as a function of the specific semantic features being (covertly) processed. The intervention of the semantic

control network in a covert semantic habituation paradigm as used in this study may reflect the progressive diminution of covert semantic monitoring processes, as the semantic control network gradually detects the predictability and the within-block semantic coherence of presented words.

Confusions between everyday objects when simultaneously available (such as between a fork and a spoon) or difficulties in retrieving the use of objects when no contextual cues are available (Jefferies and Lambon Ralph 2006; Ralph et al. 2016b; Jackson et al. 2021) as observed in patients with semantic aphasia (SA) may be the consequence of the degradation of “automatic” semantic control. Naming or verbal fluency impairment in these patients may also stem at least partially from these control deficits. The poor capacity of SA patients to perceive subtle contextual aspects in a conversation, such as homonym discrimination, implied meaning or even humor (Jefferies and Lambon Ralph 2006; Hoffman et al. 2018), may be further aspects linked to automatic semantic control impairment. Unlike in patients with semantic dementia, cueing often allows patients with SA to perform better in various semantic tasks, clearly showing that at least some of their difficulties are related to loss of control and retrieval mechanisms rather than a loss of semantic knowledge (Chapman et al. 2020).

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

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

Finally, our results can also be considered in the light of recent computational models of the semantic system, which have integrated control and representational mechanisms (Hoffman et al. 2018; Jackson et al. 2021), unifying the Hub-and-Spoke theory (Ralph et al. 2016) and the Controlled Semantic Cognition Framework (Ralph et al. 2016b; Jefferies et al. 2020). These models also allow for dynamic properties such as recent experience buffering and conceptual learning, as well as damage caused by degeneration or stroke. The reverse-engineered model developed by Jackson et al. (2021) posits that semantic cognition relies on indirect interactions between a single deep multimodal hub (putatively the ATL) and modality-specific representational areas (spokes). Regarding control mechanisms, simulations provided significantly better results when control operated on the modality-specific areas than on its deep components (Jackson et al. 2021). This model therefore predicts that control regions should not directly connect to ATL. The present study supports this prediction, as we did not observe any significant functional connectivity between the IFG and ATL ROIs, but significant connectivity between the IFG and other category-specific representational areas. Moreover, Hoffman et al. proposed a computational model combining a Hub-and-spokes architecture with a

“buffer” system that allows activated semantic information to be influenced by current context; this interaction between semantic knowledge and context has been proposed to be supported by the ventral parietal cortex (VPC). The strong and persistent neural responses we observed in ventroparietal cortex (AG) may support this prediction as the AG response pattern differed from the other semantic ROIs in that it was neither specific to semantic knowledge nor to control.

Conclusions

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

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Notes

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