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A dual architecture for the cognitive control of language: Evidence from functional imaging and language production

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ABSTRACT

The relation between language processing and the cognitive control of thought and action is a widely debated issue in cognitive neuroscience. While recent research suggests a modular separation between a ‘language system’ for meaningful linguistic processing and a ‘multiple-demand system’ for cognitive control, other findings point to more integrated perspectives in which controlled language processing emerges from a division of labor between (parts of) the language system and (parts of) the multiple-demand system. We test here a dual approach to the cognitive control of language predicated on the notion of cognitive control as the combined contribution of a semantic control network (SCN) and a working memory network (WMN) supporting top-down manipulation of (lexico-)semantic information and the monitoring of information in verbal working memory, respectively. We reveal these networks in a large-scale coordinate-based meta-analysis contrasting functional imaging studies of verbal working memory *vs.* active judgments on (lexico-)semantic information and show the extent of their overlap with the multiple-demand system and the language system. Testing these networks' involvement in a functional imaging study of object naming and verb generation, we then show that SCN specializes in top-down retrieval and selection of (lexico-)semantic representations amongst competing alternatives, while WMN intervenes at a more general level of control modulated in part by the amount of competing responses available for selection. These results have implications in conceptualizing the neurocognitive architecture of language and cognitive control.

1. Introduction

Humans' signature skills for elaborate language have long been associated with their higher-level executive functions – in particular cognitive control or the top-down processing of information for organized behavior (Alexander et al., 1989; Fuster, 2015; Levelt, 1989; Badre and Wagner, 2007; Koechlin and Summerfield, 2007; Goldberg, 2009; Novick et al., 2010; Fedorenko, 2014; Geranmayeh et al., 2014; Lambon-Ralph et al., 2017; Rouault and Koechlin, 2018). Cognitive control enables speakers-listeners to integrate novel information internally and independently from immediate context, contributing to the inherent generative properties of everyday language use (Goldberg, 2009; Fuster, 2015). Still, the exact mechanisms subserving the cognitive control of language remain a matter of debate. This debate centers on whether these mechanisms operate at the core of the cortical language network or intervene peripherally to regulate top-down information integration. Elucidating this issue naturally requires a comprehensive account of the neurocognitive systems underlying linguistic processing (Fedorenko and Thompson-Schill, 2014), but equally relevant is a detailed characterization of the neural underpinnings of cognitive control, its basic psychological laws and the way in which they could service the needs of language comprehension and production. The present study aims to contribute new evidence to this research program.

A prominent perspective on the relation between language and cognitive control has arisen from a series of large-scale functional imaging (fMRI) studies suggesting a modular divide between a ventral *language system* responsible for the lexical and combinatorial processing of words and sentences, and a dorsal *multiple-demand system* recruited in several cognitive tasks requiring key executive functions such as attention and working memory[1] (Fedorenko et al., 2011, 2013; Duncan, 2001, 2013). The separability between language and cognitive control is suggested from the observation that most regions within the language system are not activated by tasks involving the multiple-demand system (Fedorenko et al., 2011). This separation still leaves open the possibility for both systems to interact whenever circumstances require top-down control over information integration, as has been argued to occur

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[1] We point out here that attention is now conceptualized as integral to working memory rather than separate from it. More particularly, most recent advances in the study of working memory have led to its characterization as the temporary allocation of attention to behaviorally relevant representations (cf. Postle, 2006).

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during language production (Fedorenko, 2014; Hagoort, 2005; Levelt, 1989). Evidence that prefrontal regions associated with language and cognitive control (e.g. Broca's area) comprise adjacent sections of the language system and the multiple-demand system lends further credence to this hyopthesis while maintaining the modular separation between the neurocognitive bases of language and organized behavior (Fedorenko et al., 2012, see also Hagoort, 2005).

This modular perspective however contrasts with substantial research indicating that several regions within the language system itself subserve several functions typically subsumed under cognitive control. Two areas in particular – the posterior middle temporal gyrus (pMTG), usually considered the the prime substrate of lexical storage and access (Lau et al., 2008), and the ventrolateral prefrontal cortex (vLPFC) – have been shown to support top-down retrieval and selection of (lexico-)semantic representations from competing alternatives (Badre et al., 2005; Bourguignon et al., 2018; Davey et al., 2016 Badre and Wagner, 2007; Lau et al., 2008; Lambon Ralph et al., 2017). They have recently been described as part of a ‘semantic control network’ responsible for the top-down manipulation of (lexico-)semantic knowledge for language amongst other complex behaviors (Jefferies, 2013; Lambon Ralph et al., 2017). Crucially, this network is known to operate in concert with the dorsolateral prefrontal cortex (dLPFC) and inferior parietal lobule (IPL) when semantic processing takes place under increased demands for attention and working memory (Whitney et al., 2011; Nagel et al., 2008, see also Davey et al., 2016). These findings suggest a ‘graded’ architecture of cognitive control, whereby ventral sectors of the brain specialize in the cognitive control of (lexico-)semantic memory, while its dorsal sectors intervene at a more general level in attention allocation and maintenance of information in working memory (Lambon Ralph et al., 2017).

This graded architecture downplays a modular separation between language and cognitive control in favor of a distributed approach to cognitive control as an emergent property of (at least) two parallel networks connecting different sectors of the frontal lobes to posterior associative regions (Petrides, 2005; Badre and D'Esposito, 2009). Extant architectonic and functional imaging evidence in particular indicates that dLPFC supports the ‘monitoring of information in working memory’, while vLPFC subserves ‘active judgments on information held in posterior cortical association regions that are necessary for active retrieval and encoding of information’ (Petrides, 2005, p. 781). The idea that such networks should ‘be involved in all types of cognitive processing (…) and, in the more complex human brain, will be adapted for use in linguistic (…) processing’ (*op. cit.* p. 792) further reinforces this parallel and attributes to precisely identifiable regions of the language system and multiple-demand system distinct sub-functions of controlled language processing, in particular active judgments on (lexico-)semantic information in vLPFC and pMTG (i.e. the semantic control network) and the monitoring of information in verbal working memory in dLPFC and IPS.

Here we examined this dual-network approach in two complementary phases. In a first phase (Phase I), we carried out an extensive coordinate-based meta-analysis of 163 functional imaging studies published in the neuroscific literature on cognitive control and contrasted in particular brain activations associated with active judgments on (lexico-)semantic information (96 studies) against those associated with the monitoring of information in verbal working memory (67 studies). Expanding upon previous meta-analyses centered on the neural correlates of semantic control (e.g. Noonan et al., 2013) and working memory (e.g., Smith and Jonides, 1999; Rottschy et al., 2012), this contrastive analysis was used to confirm the existence of a working memory network (WMN) and a semantic control network (SCN) and to assess the extent to which they form part of the multiple-demand system and the language-system, respectively.

In a second phase (Phase II), we used functional regions of interest constructed from the activation patterns obtained in Phase I in a re-analysis of fMRI data obtained in tasks of overt object naming and verb generation (Bourguignon et al., 2018) with a view to gain deeper understanding of the contribution of SCN and WMN in the cognitive control of language production. As explained above, spoken language figures amongst the most salient instances of controlled language processing owing to its underlying requirements for top-down information integration (Fedorenko, 2014; Fedorenko and Thompson-Schill, 2014; Levelt, 1989). In this respect, object naming and verb generation tasks lend themselves particularly well to studying the cognitive control of language for two reasons. First, both object naming and verb generation involve a basic operation of cognitive control: the selection of responses amongst competing alternatives (Thompson-Schill et al., 1997; Kan and Thompson-Schill, 2004; Edwards et al., 2010; Bourguignon, 2014; Bourguignon et al., 2018). Substantial research has shown that the number of names competing for the same object (e.g. *sofa*, *settee*, *couch*) or the number of verbs that can be semantically associated with this object (e.g. *sit*, *lie*, *relax*) strongly predict variance in language production latencies (Lachman, 1973; Alario et al., 2004; Severens et al., 2005; Bourguignon et al., 2018), parallelling earlier behavioral evidence for an association between response competition and the cognitive resources deployed to resolve it (Berlyne, 1957). Interestingly, this association has been captured by the information-theoretic concept of entropy (H)

$$H = -\sum_{i=1}^{N} p_i \log_2 p_i \tag{1}$$

summing the inverse log-probabilities p of the words $i \dots N$ produced in response to a stimulus (Lachman, 1973; Alario et al., 2004; Severens et al., 2005, Bourguignon et al., 2018). Entropy is of particular relevance here given its characterization as a key psychological law of cognitive control (Berlyne, 1957; Koechlin and Summerfield, 2007; Bourguignon, 2014) and its exploitation as a predictor of prefrontal activity associated with the selection of behaviorally relevant representations amongst competing alternatives (Koechlin et al., 2003, 2007; Yoshida and Ishii, 2006). In a recent study (Bourguignon et al., 2018), we were able to show that entropy similarly captures the neural dynamics of (lexico-)semantic selection in the prefrontal cortex during language production, highlighting in particular the existence of a task-related posterior-anterior gradient of selection processes from object naming to verb generation in the vLPFC. This result however is restricted to brain activations confined in the prefrontal cortex, overlooking the possibility for entropy to predict and tease out competition-related activations at the systems-level. To bridge this gap, we utilized entropy to test the hypothesized contribution of SCN and WMN in the cognitive control of language. More specifically, to the extent that response entropy during object naming and verb generation captures selection competition at a (lexico-)semantic level of representation (Bourguignon et al., 2018), we expected it to covary with trial-based blood oxygen level dependent (BOLD) signal changes primarily within SCN but not within WMN.

Second, several mechanistic differences between object naming and verb generation besides their common selection requirement should help reveal task-related effects of (lexico-)semantic retrieval and working memory monitoring on the neural dynamics of SCN and WMN (see Noonan et al., 2013 for earlier research on this topic). In particular, (lexico-)semantic information is assumed to be automatically accessed in object naming to the extent that the object's identity is immediately recognized through perceptual systems and only its name needs to be selected from a limited set of competitors (Etard et al., 2000; Bourguignon, 2014). In contrast, verb generation requires top-down information retrieval because the object perceived is insufficient in itself to access the broad range of semantically associated verbs. Furthermore, this increased number of competing responses in verb generation should exert significant demands on WMN (Gabrieli et al., 1998; Nagel et al., 2008). We therefore expected substantially stronger involvement of pMTG for top-down lexico-semantic retrieval and of dLPFC and IPS for working memory monitoring during verb generation compared to object naming. Altogether, these investigations should shed significant light on the relation between language and cognitive control and have key implications for understanding the neurocognitive underpinnings of human behavior.

2. Phase I: an ALE analysis of brain systems for controlled (lexico-)semantic processing *vs.* working memory monitoring

In Phase I we aimed to contrast brain activations reported in functional imaging studies examining active judgments on (lexico-)semantic information *vs.* monitoring of information in verbal working memory. We also examined the extent to which these activations intersect with the language network and the multiple-demand network, respectively. To this end, we used an updated and corrected version of activation likelihood estimation analysis methods (ALE, cf. Eickhoff et al., 2012, 2017, available on http://brainmap.org/ale) enabling identification of activation clusters across functional imaging studies through probabilistic distribution of significant activation loci while controlling for inter-studies distributional uncertainty. The activation patterns originating from this analysis provided the basis for the construction of functional regions of interest to be used in Phase II (see below).

2.1. Methods

The studies entered into the ALE analysis were culled from ten published reviews and meta-analyses addressing the neurocognitive correlates of cognitive control (Ridderinkhof et al., 2004; Koechlin and Summerfield, 2007), working memory (D'Esposito et al., 1998; Smith and Jonides, 1999; Owen et al., 2005; Rottschy et al., 2012) and controlled semantic processing (Badre and Wagner, 2007; Binder et al., 2009; Noonan et al., 2013). They were selected according to the following inclusion/exclusion criteria: (1) Only studies utilizing fMRI or PET and reporting group averaged space coordinates (MNI or Talairach) were included, (2) from these studies, only those that investigated active judgments on (lexico-)semantic information or the monitoring of information in verbal working memory were taken into consideration (cf. point **1.1** in supplementary information for a description of the tasks used in each of these studies), (3) studies addressing ancillary processes related to motivation, emotion, visuospatial processing, stimulus encoding without subsequent decisions or that addressed questions related to second language processing were excluded. (4) Although every experimental paradigm designed to study a given cognitive process inevitably involves some degree of working memory monitoring (if only to maintain task instructions), care was taken to minimize confounds between (lexico-)semantic processing and working memory demands by excluding paradigms that combined (lexico-)semantic judgment tasks with classical experimental paradigms of working memory (e.g. delayed task, cf. Fiebach et al., 2007). (5) Only contrasts performed on unrepeated stimuli were considered and (6) studies involving clinical populations were screened to keep results obtained in healthy controls only. This criterion excluded direct contrasts between control and clinical participants. A total of 163 studies met the above criteria, including 96 studies on active judgment on (lexico-)semantic information (cf. Table S1A in supplementary information) and 67 studies on monitoring of information in working memory (cf. Table S1B in supplementary information). Foci reported in MNI stereotaxic space were converted into Talairach space coordinates using the Convert Foci tool implemented in GingerALE. When more than one legible contrast was available in the same study, only one contrast was randomly selected to avoid sampling biases. In total, 758 foci were collected over 1323 participants for the (lexico-)semantic studies (henceforth: LS), and 747 foci were collected over 933 participants for the working memory studies (henceforth: WM). Although the number of studies and participants appears to differ substantially between LS and WM studies, the most important contributor to ALE results is the number of foci included (Turkeltaub et al., 2012), which was largely similar between LS (758) and WM studies (747). The foci for LS and WM studies were separately entered into first-level random-effects Turkeltaub Non-Additive ALE analyses minimizing within-experiment and within-group effects on the computation of probabilistic maps (Turkeltaub et al., 2012). Analysis parameters were set at a cluster-level inference threshold of $P = 0.01$ (1000 thresholding permutations) and an uncorrected cluster forming value of $P = 0.001$. A second-level analysis then contrasted first-level maps with a False Discovery Rate of $q \leq 0.05$. The resulting clusters were then screened for false positives by setting a minimum of two contributing foci for each cluster.

The resulting contrast maps for LS (LS > WM) and WM studies (WM > LS) were then respectively overlaid against the language network (LANG) map (available at https://evlab.mit.edu/papers/Mahowald_NI) and the multiple-demand network (MD) map (available at http://imaging.mrc-cbu.cam.ac.uk/imaging/MDsystem), and functional regions of interest (fROIs) were created based on the areal intersection between the LS and LANG maps ([LS > WM] ∩ LANG) and between the WM and MD maps ([WM > LS] ∩ MD). This was done using the ROI tool implemented in the Multi-Image Analysis GUI (Mango, available at http://ric.uthscsa.edu/mango/).

2.2. Results and discussion

Results from the ALE analyses are displayed in Fig. 1 and corresponding anatomical information is provided in Table 1. Overall, they confirm that the monitoring of information in verbal working memory involves a dorsal activation pattern comprising dLPFC and IPS, while active judgments on (lexico-)semantic memory engage a ventral activation pattern including vLPFC and pMTG. Both patterns included additional regions often reported in relation with (lexico-)semantic processing and verbal working memory and exhibited substantial overlap with the language system and the multiple-demand system, respectively. We describe these findings in detail below.

The first-level maps for the studies involving active judgments on (lexico-)semantic information (LS, $N = 96$) and those involving verbal working memory monitoring (WM, $N = 67$) revealed two broad activation patterns following the expected dorso-ventral subdivision: LS was associated with activation in the ventral portion of the lateral prefrontal cortex, the posterior section of the left middle temporal lobe and the angular gyrus (cf. Fig. 1A left, Table 1A), while WM involved activation in the dorsal portions of the left and right lateral prefrontal cortex, the superior and inferior portions of the left and right parietal lobes as well as left and right pre-motor, cingular and insular regions (cf. Fig. 1A right, Table 1B). Second-level contrasts between LS (Fig. 1B violet, Table 1C) and WM (Fig. 1B yellow, Table 1D) largely conserved these separate activation patterns. We then assessed the degree of respective areal intersection between the LS pattern and the language system reported in Fedorenko et al. (2011) on the one hand, and between the WM pattern and the multiple-demand system (MD) reported in Fedorenko et al. (2013) on the other. As shown in Fig. 1C, the LS > WM contrast map overlapped substantially with the language system (violet), while most of the WM > LS map intersected with the multiple-demand system (yellow).

It has been suggested that the multiple-demand system consists of two complementary subnetworks responsible for different aspects of general cognitive control (Dosenbach et al., 2007; Duncan, 2013). In particular, its dorsolateral prefrontal and parietal sectors are taken to support the online maintenance of control signals in working memory on a trial-to-trial basis, while regions in and around the anterior cingulate cortex, the anterior insula and pre-motor cortex are described as part of a cingulo-opercular network (CON) contributing to trial- and task-based information integration (Dosenbach et al., 2007, 2008). This putative subdivision is of interest because WMN and CON may differentially contribute to the cognitive control of language production (Geranmayeh et al., 2014; Bourguignon et al., 2018). Following previous research (Geranmayeh et al., 2014; Bourguignon et al., 2018), we therefore partitioned the WM ∩ MD map (cf. Fig. 1C yellow) into regions included in the CON, namely the anterior cingulate cortex, the left anterior insula and left and right dorsal and ventral premotor cortices (Fig. 1D cyan) and

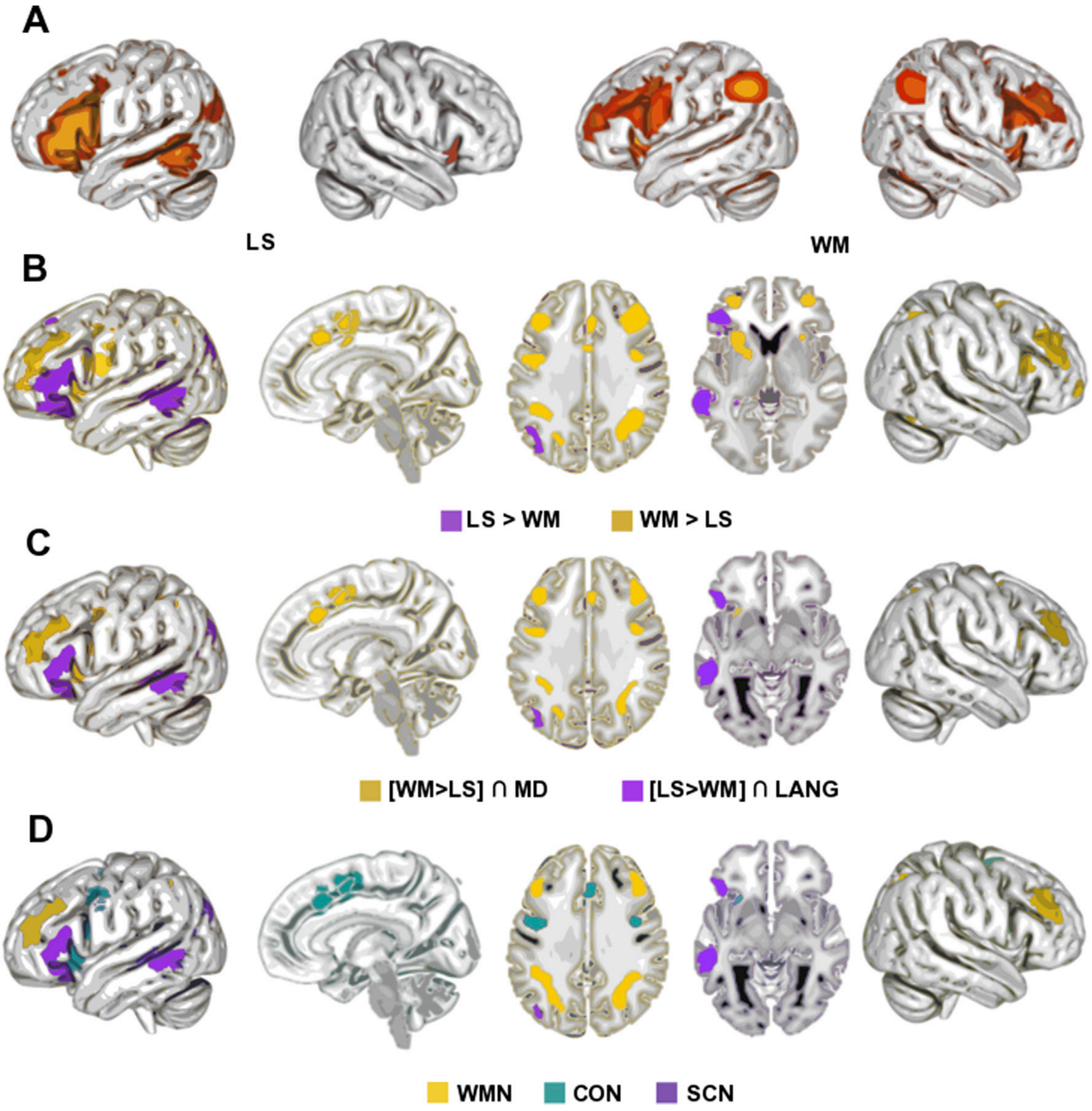

Fig. 1. Results from the ALE analysis (cf. Table 1 for detailed stereotaxic information). (**A**) First-level ALE maps for (lexico-)semantic (LS) studies (left) and working memory (WM) studies (right, cf. Table 1A/B). (**B**) Second-level contrast between LS studies (violet) and WM studies (yellow, cf. Table 1C/D). (**C**) Extent of areal overlap between ALE maps obtained in the LS > WM contrast and Fedorenko et al. (2011) language system (violet) and ALE maps obtained in the WM > LS contrast and Fedorenko et al. (2013) multiple-demand system (yellow). (**D**) Anatomical parcellation of the maps represented in (**C**) into a working memory network (WMN, yellow) and a cingulo-opercular network (CON, cyan), both of which have been described as sub-components of the multiple-demand network (Dosenbach et al., 2007, 2008; Duncan, 2013), and a semantic control network (SCN, violet). The clusters contained within each of these networks were used as functional regions of interest for the fMRI analysis of ON and VG.

regions included in WMN, comprising the left and right inferior parietal lobules and left and right dorsolateral prefrontal cortices (Fig. 1D yellow). These two networks were considered along SCN, comprising the posterior aspect of the left middle temporal gyrus, the left angular gyrus and the left ventrolateral prefrontal cortex (Fig. 1D violet, cf. Table 2 for detailed anatomical information). The clusters within each network were then used as functional regions of interest (fROIs) for the fMRI analyses of the ON and VG tasks.

3. Phase II: functional imaging experiment on object naming and verb generation

In Phase I of the present study (cf. **2**) we aimed to uncover the primary brain systems assumed to drive the cognitive control of language processing, in particular active judgments on lexico-semantic information in SCN on the one hand and the monitoring of information in verbal working memory in WMN on the other. Additionally, we sought to probe the extent of the respective overlap between SCN and WMN and the putative 'language system' (LS) and 'multiple-demand system' (MD) reported in Fedorenko et al. (2011, 2013). The most important finding obtained at this point is that SCN is effectively part of LS, suggesting that LS does participate in the cognitive control of lexico-semantic information, while MD rather contributes to the monitoring of information in verbal working memory. Expanding upon this finding, the aim of Phase II was to further examine the involvement of each fROI identified in the ALE analyses (Phase I) in a reanalysis of previously published fMRI data investigating the neural dynamics of cognitive control during object naming and verb generation tasks (Bourguignon et al., 2018). Additionally, this research enabled deeper examination of task differences in the requirement for top-down retrieval of (lexico-)semantic representation and monitoring of information in verbal working memory, expecting in particular that this requirement should be increased in VG compared

Table 1

(A-B) Cluster information from the first-level ALE maps for the LS studies (A, cf. Fig. 1 left) and WM studies (B, cf. Fig. 1 right). (C-D) Cluster information from the contrasts LS > WM (C, Fig. 1B violet) and WM > LS (D, Fig. 1B yellow). Stereotaxic coordinates are given in the Talairach atlas fitted onto the MNI152 standard space. Legend: Hemi = hemisphere, BA = Brodmann's area, pMTG = posterior middle temporal gyrus, v/dLPFC = ventro/dorsolateral prefrontal cortex, MFG = middle frontal gyrus, AG = angular gyrus, PCG = precentral gyrus, MFG = dorsal middle frontal gyrus, S/IPL = superior/inferior parietal lobe, SFG = superior frontal gyrus, ACC = anterior cingulate cortex, Ant. Ins. = anterior insula, IFG = inferior frontal gyrus, PCG = precentral gyrus.

Cluster	Hemi	BA	Size, mm^3	Centroid			Peak			Peak *P*
				x	*y*	*z*	*x*	*y*	*z*	
(A) ***LS***										
vLPFC	L	46/47	52 672	−43.2	21.5	11.6	−44	20	20	0.04
pMTG	L	21	28 872	−46.8	−41.7	−10	−56	−42	−4	0.03
SFG	L	6	19 080	−5.3	17.1	47	−4	10	50	0.02
AG	L	39	12 272	−38.9	−65.2	32.7	−44	−68	26	0.01
Ant. Ins.	R	13/47	6 464	34	23	03	32	22	2	0.01
(B) ***WM***										
dLPFC	L	10/9/6	56 888	−38.7	14.2	20	−44	8	24	0.03
dLPFC	R	9/10	30 736	39.9	25.3	20	38	34	30	0.02
SFG	R	6	22 272	4.1	13.5	45.1	2	10	48	0.03
SPL/IPL	L	7/40	18 104	−33	−54.4	40.7	−30	−58	40	0.03
SPL	R	7	13 824	33.6	−55.9	41.2	32	−58	42	0.02
(C) ***LS > WM***										**Extrema**
vLPFC	L	47	9 344	−43.9	30.5	−1.9	−42.7	32.4	−4.3	3.9
pMTG	L	37/21	6 208	−57.7	−39.2	−5.5	−60.8	−38.6	−4.9	3.9
AG	L	39	3 288	−42.7	−66.2	26.1	−42.6	−59.4	22.2	3.7
SFG	L	8	1 288	−12.2	32.7	46.1	−11	35.7	46	3.7
(D) ***WM > LS***										
SPL/IPL	R	40/7	11 144	33.2	−56	41.1	31.6	−57.1	40.5	3.9
SPL/IPL	L	40/7	9 856	−35	−50.7	40.4	−40.4	−43.3	39.2	3.9
MFG	R	10	8 056	38.6	32.8	30.8	38.6	32.7	32.5	3.9
Claustrum	L	–	6 696	−25.1	10	3.8	38.6	32.7	32.5	3.9
PCG	L	6	6 648	−48.1	0.4	25.9	−50.7	−0.2	22	3.9
MFG	L	10	6 496	−36.1	41.9	18.4	−37	40.4	21.6	3.9
SFG/ACC	R	6/24	5 920	14.9	5.7	49.8	21.5	5.5	54.7	3.9
ACC	–	32	1 384	2.5	26.7	35.4	2	27	34	3.7
MFG	R	10	1 368	34.1	50.5	1.7	34	51	−0.7	3.9
IFG	R	45	1 200	54.4	13.9	19.1	58	13	18	3.5
PCG	R	6	1 048	39.4	2.6	30.6	38.3	−1	31.8	3.9
PCG	L	6	472	−28	−6.8	54.9	−26	−10	50	2.9
Claustrum	R	–	192	29.3	17.1	1.8	29	16	2	2.7
Thalamus	L	–	176	−16.8	−13.5	14.7	−18	−14	14	2.7

Table 2

Anatomical specifics of the functional regions of interest (fROIs) and associated cortical networks used in the fMRI analyses of object naming and verb generation. These fROIs were obtained after intersecting the LS and WM maps obtained in the ALE analyses and the language and multiple demand networks reported in Fedorenko et al., (2011), 2013 studies, respectively, then partitioning the resulting maps into the semantic control network (SCN, cf. Fig. 1D, violet), the working memory network (WMN, cf. Fig. 1D, yellow) and a cingulo-opercular network (CON, cf. Fig. 1D, cyan). pMTG = posterior middle temporal gyrus, AG = angular gyrus, vLPFC = ventrolateral prefrontal cortex, IPL = inferior parietal lobule, dLPFC dorsolateral prefrontal cortex, d/vPCG = dorsal/ventral precentral gyrus, dACC = dorsal anterior cingulate cortex. Stereotaxic coordinates are given in the Talairach atlas fitted onto the MNI152 standard space.

fROI	Hemi	Volume mm^3	Center of mass		
			x	y	z
SCN					
pMTG	L	4 176	−58	−38	−2
AG	L	2 584	−44	−66	26
vLPFC	L	3 600	−46	22	−8
WMN					
IPL	L	9 232	−34	−50	42
IPL	R	9 592	32	−56	44
dLPFC	L	4 256	−38	42	24
dLPFC	R	4 808	38	34	28
CON					
dPCG	L	472	−30	−6	56
dPCG	R	1 704	24	2	56
vPCG	L	2 792	−44	2	34
vPCG	R	984	38	4	32
dACC	–	1 824	6	10	50
Ant.Ins.	L	2 512	−30	18	4

to ON.

3.1. *Methods*

3.1.1. *Participants*

The study included sixteen healthy, right-handed (Oldfield, 1971) native speakers of English (8 males, age 19–29), who took part in 30-min scanning sessions under informed consent and in return for monetary compensation. The study was conducted at the Montreal Neurological Institute (Quebec, Canada) in accordance with the ethical standards of the 1964 Declaration of Helsinki and the requirements of the McGill Faculty of Medicine Ethics Review Board.

3.1.2. *Tasks and procedures*

Participants took part in an overt object naming task (ON) and an overt verb generation task (VG) while their brain activity was concomitantly monitored using fMRI (cf. **3.1.5** and **3.1.6** for detail). A word reading task was also part of the experiment to probe into the motor aspects of speech production and its results are discussed in Bourguignon et al. (2018).[2] Stimuli consisted in ninety black-and-white drawings and their associated written names taken from the normed materials of Snodgrass and Vanderwart (1980, cf. supplementary information for a complete list of the stimuli used). Although modified versions of Snodgrass and Vanderwart's materials have been shown to influence several aspects of naming performance (Rossion and Pourtois, 2004), existing

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[2] Since the stimulus materials for the word reading, ON and VG tasks were balanced across three experimental lists, it was possible to carry out an analysis of ON and VG while excluding word reading.

norms for verb generation performance were only available for the original materials (Kurland et al., 2014). The pictures were distributed across three experimental lists randomly assigned to participants and constructed so that one stimulus used for VG did not reappear in ON within the same list and vice versa. In total, each participant therefore saw thirty unique pictures for each task. Participants across lists were matched for age, verbal IQ (Wechsler, 1999), performance IQ (Raven et al., 2003) and handedness (Oldfield, 1971, cf. Table S2 in supplementary information for demographic information). Pictures for each task were randomly distributed across three ten-trial runs interspersed along with the reading runs with shorter runs of rest (thirty rest trials in total for each list), in which participants remained silent and kept their eyes fixed on a black screen. ON, VG and rest runs began with the instructions NAME, VERB and REST, respectively. For ON, participants were required to produce the name of the object represented on the picture. In VG, they were required to produce a verb semantically related with the object represented on the picture. Participants were asked to provide their responses as quickly and as clearly as possible during a 3 second silent time-window or to say ‘I don't know’ when they could not find a response within the allotted 3 seconds. The order of runs was pseudo-randomized and counter-balanced across lists.

3.1.3. *Entropy measures of response selection*

Response entropy for ON and VG was taken from the norms of Snodgrass and Vanderwart (1980) and Kurland et al. (2014), respectively. Response entropy was computed with the equation featured in the **Introduction**. To provide a working example of how this equation is used, let us assume that six participants out of ten ($p = 6/10 = 0.6$) produce the word ‘panther’ for the picture of a panther, whilst the remaining four participants ($p = 4/10 = 0.4$) produce the word ‘cheetah’, response entropy for this picture is then calculated as $-[(0.6 \times \log_2 0.6) + (0.4 \times \log_2 0.4)] = 0.97$. The same equation was used to compute entropy for VG (Kurland et al., 2014). There was no noticeable relationship between response entropy in ON and response entropy in VG ($R < 0.15$, $P > 0.15$). Care was taken that stimulus lists were matched in terms of response entropy for ON and VG so as not to make one list more competitive than the other two. In addition, the pictures across lists were matched on image agreement, visual complexity and concept familiarity (Snodgrass and Vanderwart, 1980) as well as age of acquisition (Kuperman et al., 2012) and frequency of the object name (Brysbaert and New, 2009, cf. Table S3 in supplementary information for means on these measures across stimulus lists).

3.1.4. *Behavioral data analysis*

The behavioral data for this dataset were already reported and discussed in Bourguignon et al. (2018) and will therefore not be discussed in detail here save for a brief recapitulation of the main findings and their implications for fMRI analysis as well as some additional observations worthy of attention (see also Table S4 in the supplementary information).

3.1.5. *Data acquisition*

A sparse-sampling protocol was utilized for fMRI acquisition, enabling concomitant recording of overt verbal responses and trial-based volume acquisition while minimizing head-movement artifacts (Gracco et al., 2005). Pictures were presented on a projector screen for 3 seconds, during which the MR gradients were turned off and participants were asked to speak their responses recorded with an MR compatible microphone attached to the head coil (Optoacoustics, Yehuda, Israel). A 0-to-500 ms random time jitter preceded picture onset. After the picture disappeared, the screen remained black for an additional 1.5 seconds (adjusted for the preceding time jitter), then the MR gradients were turned on for 2 seconds. The TR for each trial therefore had a total duration of 6.5 seconds, allowing sufficient time for the hemodynamic response to reach its peak before volume acquisition. One volume was acquired for each trial. The thirty volumes acquired during rest were used to compute an average rest baseline. Head movement was minimized by immobilizing participants' head with a polystyrene-filled vacuum bag and a forehead restraining device. Participants were also briefed and trained on an abbreviated version of each task a few days before scanning using different pictures.

3.1.6. *MR data acquisition and pre-processing*

MR image acquisition was performed on a 3T Siemens Magnetom TrioTim scanner. Participants lay supine on the scanner table while structural images of their brains were acquired with a T1-weighted 3D MPRAGE sequence (TR = 2.2. seconds, TE = 2.98 seconds, slice thickness 1 mm, voxel-size = 1 × 1 × 1 mm, flip-angle = 9°, FOV = 256 × 256 mm). Functional images were then acquired during ON and VG using a T2*-weighted EPI sequence functional scan (33 interleaved axial slices, slice thickness = 4 mm, in-plane resolution 64 × 64 mm, TR = 6.5 seconds, delay in TR = 4.5 seconds, TE = 30 ms, flip-angle = 90°, FOV = 256 × 256 mm). Data were pre-processed using FSL 5.0.9 (FMRIB, Smith et al., 2004). Preprocessing steps for each participant included motion correction (MCFLIRT, Jenkinson et al., 2002), interleaved slice-timing correction, high-pass temporal filtering (100 seconds), spatial smoothing (FWHM = 6 mm) and normalization to the MNI152 standard brain template. Head movement for each subject was computed using MCFLIRT (FMRIB, Jenkinson et al., 2002): the mean displacement of each image relative to the reference image (absolute displacement) was 0.4 mm (SD = 0.22) and the mean displacement of each image N relative to the image N+1 (relative displacement) was 0.09 (SD = 0.04), indicating little movement during scanning (below voxel size).

3.1.7. *Controlling for task differences in cognitive demands*

As explained in the **Introduction** (see also Kurland et al., 2014; Bourguignon et al., 2018), response entropy for the same stimulus list is on average significantly higher in VG than in ON (in the present case, $M_{VG} = 2.06$ *vs.* M_{ON} 0.56, comparison $t = 10.347$, $P < 0.001$). This difference in the number of responses available per individual trial has led to the general view of VG as cognitively more challenging than ON (Kurland et al., 2014; Edwards et al., 2010; Bourguignon, 2014). To the extent that response entropy is calculated based on the number of responses produced for the same object, it may therefore additionally capture variations in the level of effort deployed to monitor competing responses in verbal working memory. However, the cognitively challenging nature of VG compared to ON can also be attributed to other factors that do not bear a direct relation with response competition. Amongst these figure task-level inhibitory processes whereby participants suppress a prepotent tendency to name the object in order carry out the less automatic task of generating a verb (an effect germane to the Stroop task), variations in the strength of semantic association between objects and candidate verbs (i.e. weak object-verb associations are presumably more difficult to retrieve than strong object-verb associations) and other processes possibly related to grammatical encoding (e.g. establishing thematic relations between objects and verbs, cf. Kurland et al., 2014). These co-existing factors make it difficult to single out how much of selection-related brain signal is accounted for by response competition. More generally, the relation between response competition and related cognitive demands has been a notoriously difficult issue in cognitive control research. While it makes intuitive sense that more competitive stimuli should be characterized as cognitively more challenging, other authors have suggested that response competition and related cognitive effort should be dissociated (Koechlin et al., 2003; Christoff et al., 2009; Bourguignon et al., 2018). Under the general assumption that cognitive effort is reflected in variations in participants' response latencies (Demb et al., 1995; Christoff et al., 2009), one straightforward method for dissociating response competition from related cognitive demands at the level of brain responses is to take production latencies into account when looking at the strength of covariation between response entropy and local BOLD signal change. We discuss this method in more detail in the next two points.

3.1.8. Primary fROI analyses

The fROIs identified in the ALE analyses (Phase I) were fitted onto participants' functional images using the FLIRT tool implemented in FSL (FMRIB, Jenkinson et al., 2002). Then BOLD signal change within each fROI was extracted from participants' functional scans in ON and VG for analysis. fROI analyses proceeded in two steps. First, the involvement of each fROI in ON and VG was tested by averaging percent BOLD signal change relative to rest individually for each participant and running one sample *t*-tests corrected for multiple fROIs and tests per fROI with a false discovery rate of $P_{\mathrm{FDR}} \leq 0.05$. Only fROIs that were reliably active during ON and/or VG were considered for further analysis (see **3.2.2** for discussion on fROIs exhibiting reliable *de*-activation). Second, the involvement of active fROIs in the selection of responses amongst competing alternatives in ON and VG was examined by entering their BOLD signal change as dependent variables into partial correlations including normed response entropy as predictor variable and production latencies as covariate accounting for variations in cognitive demands (cf. **3.1.7**). Participants' partial correlation coefficients were then Fisher-transformed, averaged and entered into two-tailed *t*-tests of statistical reliability.

A potential issue in pre-selecting fROIs based on reliably positive BOLD signal and subsequently running brain-behavior correlations within these fROIs is the risk of inflating Type 1 error since more active fROIs tend to exhibit larger signal variability as a result of capturing truly active voxels in addition to noise falling in the direction of the alternative (cf. Kriegeskorte et al., 2009 supplementary information). Should this variability be accidentally correlated with the behavioral measures of interest (in the present case response entropy), statistical errors may increase in fROIs whose positive signal is due to larger amounts of noise. Several steps were taken to guard against this problem. First, signal-to-noise ratio was improved with spatial smoothing (FWHM = 6 mm). Second, the use of independently normed ON and VG entropy measures as predictor variables helped circumvent circularity between brain signal and behavioral predictors of interest acquired in the same group of participants. Third, correlation significance was adjusted for multiple testing with a false discovery rate of $P_{\mathrm{FDR}} \leq 0.05$, taking into account the number of active fROIs in ON and VG.

3.1.9. Complementary fROI analyses

Besides identifying reliable covariations between BOLD signal change and response entropy in active fROIs after partialling out production latencies (**3.1.7**), additional analyses on active fROIs that did not exhibit such covariation appeared informative in light of the task differences outlined above in relation with competition-related cognitive demands. The hypothesis tested here assumes that these fROIs should be found mainly within the multiple-demand system and that their level of activation should reflect, at least in part, the level of effort deployed to monitor competing responses in verbal working memory. This assumption implies that although response entropy may not directly predict the BOLD signal change measured in these fROIs, it may nevertheless have an indirect influence on the relation between BOLD signal change and variations in cognitive demands as measured by participants' production latencies. However, we also raised a number of additional factors likely to contribute to the cognitively challenging nature of VG, including strength of semantic association, inhibitory processes of prepotent response inhibition or other grammatical factors also captured by participants' production latencies (see especially **3.1.7**). It therefore seemed relevant to examine the extent to which the covariation between BOLD signal change and production latencies in the same fROIs may be affected by the level of selection competition reflected in response entropy. In particular, should the level of cognitive effort accounted for in the correlations between their BOLD signal change and production latencies be due to response competition, partialling out response entropy should significantly decrease these correlations. The absence of such decrease would in contrast imply that cognitive effort within the fROIs arises from task-related factors unrelated to response competition. To examine this point, the BOLD signal change obtained from active fROIs that did not directly covary with response entropy was entered as dependent variable into correlation analyses taking production latencies as independent variable with or without response entropy entered as covariate. Participants' partial correlation coefficients were then Fisher-transformed, averaged and entered into separate repeated-measures ANOVAs taking as factors of interest the number of fROIs (ON = 4, VG = 6) and the coefficient obtained with response entropy factored in or out (2 levels). The Greenhouse-Geisser correction for violations of sphericity was applied whenever appropriate.

3.2. Results and discussion

3.2.1. Behavioral results

As reported in Bourguignon et al. (2018), response latencies were reliably longer in VG compared to ON, and trial-based analyses revealed that response entropy reliably predicted participants' word production latencies in both ON and VG. Additional multiple regression analyses (cf. Table S4 in the supplementary information) confirm previous research showing that response entropy figures amongst the strongest predictors of production latencies in ON (cf. Alario et al., 2004; Severens et al., 2005) and additionally reveal that it is the only reliable predictor of production latencies in VG. The longer production latencies in VG, together with its higher response entropy scores, are consistent with the notion of VG as cognitively more demanding than ON (Kurland et al., 2014; Bourguignon et al., 2018). This discrepancy in response latencies between VG and ON was taken into account in the fROI analyses (see **3.2.3** and **3.2.4**).

3.2.2. Task-related fROI activations

Fig. 2 displays the level of BOLD signal change measured in ON and VG relative to rest within each fROI identified in the ALE meta-analysis (Phase I). Reliably active fROIs included core frontal and temporal regions of SCN and dorsolateral and inferior parietal regions of WMN. Other active fROIs were found bilaterally in CON. fROIs with reliable *de*-activation were also identified in ON, primarily within the parietal sectors of SCN and WMN. We discuss these results in detail below.

We first examined which of the fROI revealed in the ALE analyses exhibited reliable activation during ON and VG. Reliably active fROIs for both ON and VG included the left ventrolateral prefrontal cortex [L vLPFC, ON: $t_{15} = 3.09$, $P_{\mathrm{FDR}} = 0.02$, VG: $t_{15} = 6.46$, $P_{\mathrm{FDR}} < 0.001$], the left ventral premotor cortex [L vPMC, ON: $t_{15} = 8.76$, $P_{\mathrm{FDR}} < 0.001$, VG: $t_{15} = 9.11$, $P_{\mathrm{FDR}} < 0.001$], the right ventral premotor cortex [R vPMC ON: $t_{15} = 4.73$, $P_{\mathrm{FDR}} < 0.001$, VG: $t_{15} = 4.24$, $P_{\mathrm{FDR}} < 0.001$], the left anterior insula [L Ant. Ins. ON: $t_{15} = 5.99$, $P_{\mathrm{FDR}} < 0.001$, VG: $t_{15} = 8.21$, $P_{\mathrm{FDR}} < 0.001$] and the dorsal anterior cingulate cortex [dACC, ON: $t_{15} = 3.44$, $P_{\mathrm{FDR}} < 0.01$, VG: $t_{15} = 5.13$, $P_{\mathrm{FDR}} < 0.001$]. Reliably active fROIs during VG but not ON included the left posterior middle temporal gyrus [L pMTG, VG: $t_{15} = 4.88$, $P_{\mathrm{FDR}} < 0.001$], the left dorsolateral prefrontal cortex [L dLPFC, VG: $t_{15} = 4.84$, $P_{\mathrm{FDR}} < 0.001$] and the left inferior parietal lobule [L IPL, VG: $t_{15} = 3.50$, $P_{\mathrm{FDR}} < 0.001$].

In addition to fROIs exhibiting reliable activation, two fROIs exhibited reliable *de*-activation in ON: the right inferior parietal lobule [R IPL, $t_{15} = -2.62$, $P_{\mathrm{FDR}} = 0.03$] and the left angular gyrus [AG, $t_{15} = -2.78$, $P_{\mathrm{FDR}} = 0.02$]. Task-related negative BOLD signal changes have received a number of different interpretations, including energy transfer from inactive to active brain regions, neuronal suppression/inhibition or local oxygen depletion (Wade, 2002). De-activation patterns have also been identified in relation with controlled semantic processing (Krieger-Redwood et al., 2015) and language production (Seghier and Price, 2012; Geranmayeh et al., 2014), but little is yet understood about the functional significance of these patterns to explain them in relation with the questions examined here. As a result, AG and R IPL were excluded from the follow-up analyses.

3.2.3. fROI correlations with response entropy

Fig. 3 displays which fROIs reported active in **3.2.2** covaried reliably

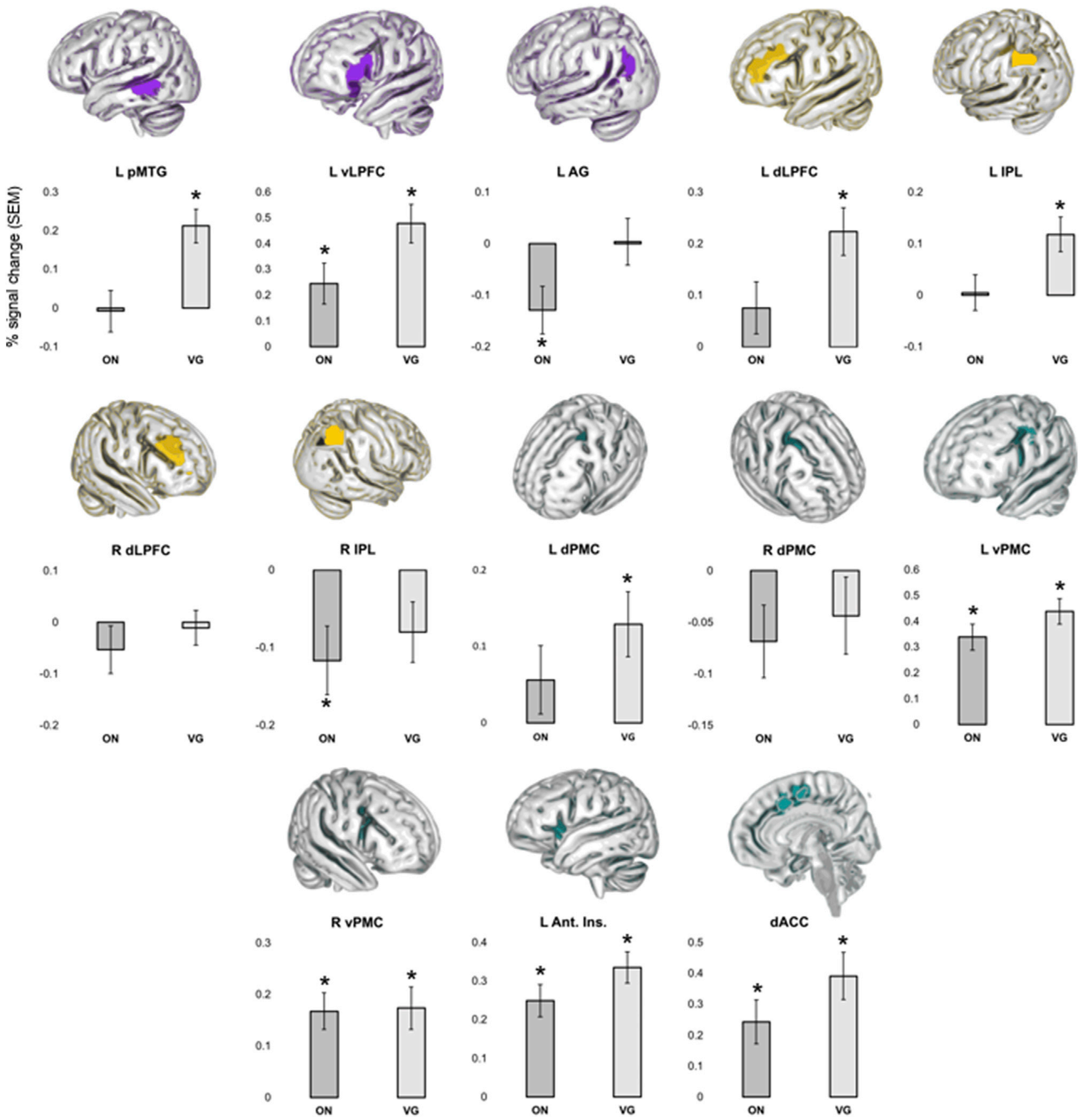

Fig. 2. Results from the functional region of interest (fROI) analysis determining task-related patterns of activation during ON and VG. Violet fROIs fall within the semantic control network (SCN), yellow fROIs within the working memory network (WMN) and cyan fROIs within the cingulo-opercular network (CON). Bar plots represent the mean percent blood oxygen level dependent (BOLD) signal change in ON (left) and VG (right) relative to rest. Error bars represent the standard error of mean (SEM). Reliability was established with two-tailed *t*-tests corrected for the total number of fROIs ($N = 13$) and tests per fROI ($N = 2$) with a false discovery rate of $^{*}P_{\mathrm{FDR}} \leq 0.05$. L pMTG = left posterior middle temporal gyrus, L vLPFC = left ventrolateral prefrontal cortex, L AG = left angular gyrus, L/R dLPFC = left/right dorsolateral prefrontal cortex, L/R IPL = left/right inferior parietal lobule, L/R dPMC = left/right dorsal premotor cortex, L/R vPMC = left/right ventral premotor cortex, L Ant. Ins. = left anterior insula, dACC = dorsal anterior cingulate cortex.

with response entropy during ON and VG while partialling out production latencies (cf. Fig. S5 in supplementary information for correlations with production latencies factored in). Reliable covariations with response entropy were observed primarily within SCN, while most fROIs within WMN and CON remained insensitive to response entropy, to the exception of L Ant. Ins. in VG. Specifically, entropy reliably predicted BOLD signal change in L vLPFC in ON [$t_{15} = 3.15$, $P_{\mathrm{FDR}} = 0.05$] and VG [$t_{15} = 2.93$, $P_{\mathrm{FDR}} = 0.03$]. Additionally, response entropy in VG predicted BOLD signal change reliably in L pMTG [$t_{15} = 2.83$, $P_{\mathrm{FDR}} = 0.03$] and L Ant. Ins. [$t_{15} = 2.98$, $P_{\mathrm{FDR}} = 0.03$] and marginally in the dACC [$t_{15} = 2.22$, $P_{\mathrm{FDR}} = 0.09$].

3.2.4. *Complementary fROI analyses: correlations with cognitive demands*

Several fROIs identified as active in the fROI identification step did not exhibit reliable covariation with response entropy after partialling out production latencies. In ON these regions included dACC, Ant. Ins. as

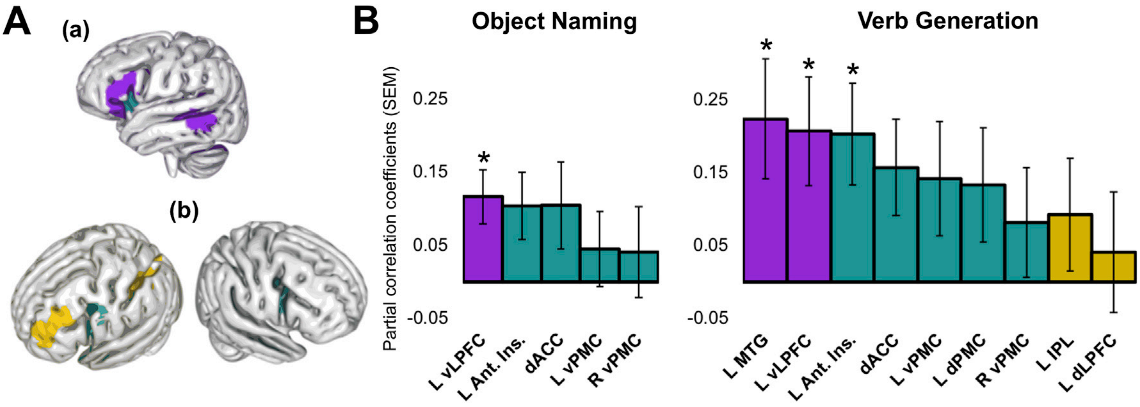

Fig. 3. (**Aa**) Active fROIs exhibiting reliable covariation with response entropy during ON and/or VG, (**Ab**) Active fROIs in ON and (cyan)/or (yellow) VG that did not exhibit reliable covariation with response entropy, (**B**) Histogram plots representing the Fisher-transformed partial correlation coefficients obtained between trial-based percent signal change and response entropy within each active fROI during ON (left) and VG (Right). Error bars represent the standard error of mean (SEM). Violet bars represent fROIs belonging to the (lexico-)semantic network, cyan bars to the cingulo-opercular network and yellow bars to the fronto-parietal network. Significance was adjusted using a false discovery rate of $*P_{\mathrm{FDR}} \leq 0.05$ taking into account the number of active fROIs in ON ($N = 5$) and VG ($N = 9$).

well as vPMC bilaterally. In VG these included dACC, L dLPFC, L dPMC, vPMC bilaterally and L IPL. That these regions did not respond directly to variations in response entropy despite being reliably active denotes their role at another, more general level possibly driven by the degree of response competition of each stimulus presented in ON and VG, exerting significant demands for the monitoring of these competitors in verbal working memory or to other factors susceptible to participate in the cognitively challenging nature of these tasks, especially VG (cf. **3.1.7**). To probe the extent of the effect of stimulus competition *vs.* other sources of cognitive demands on the activity of these fROIs, we performed additional analyses between their BOLD signal change and production latencies with or without response entropy included as a covariate.

The results from these analyses are displayed in Fig. 4. For ON, the strength of the covariation between BOLD signal change and participants' production latencies did not reliably change whether response entropy was partialled in (Fig. 4A) or out (Fig. 4B) of the correlation [main effect

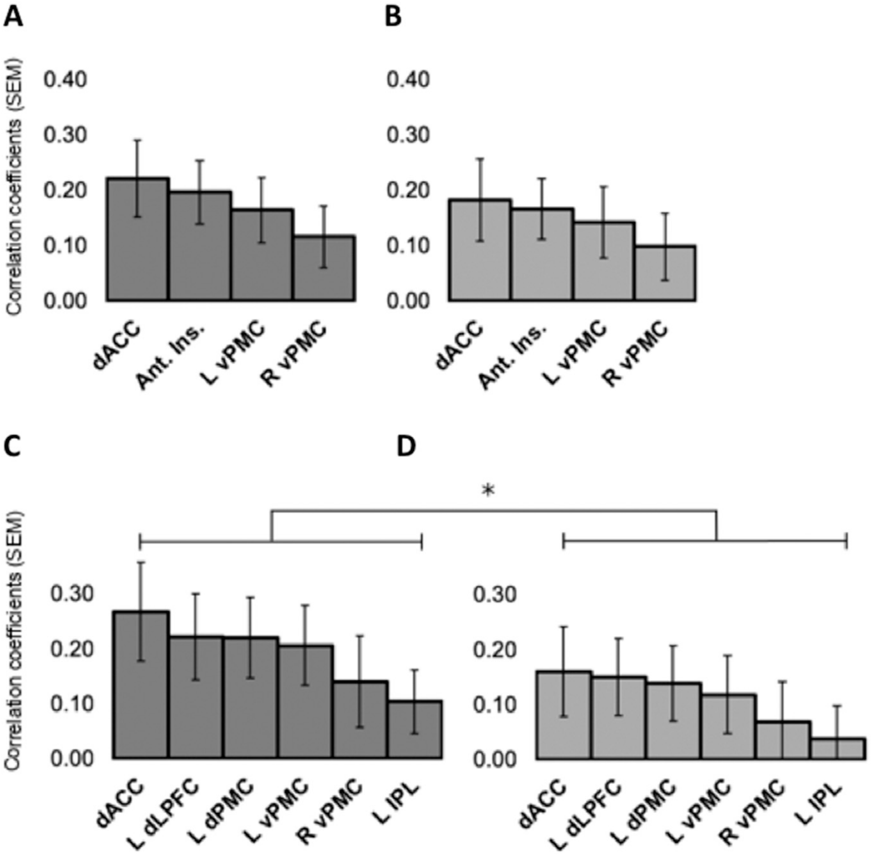

Fig. 4. Fisher-transformed correlation coefficients between BOLD signal change and participants' production latencies in ON (**A-B**) and VG (**C-D**) partialling response entropy in (**A - C**) and out (**B - D**) as a covariate. Statistical significance was adjusted for violations of sphericity with Greenhouse-Geisser correction$*P_{\mathrm{G\text{-}G}} \leq 0.05$. Error bars represent the standard error of mean (SEM).

of coefficient $F_{1,15} = 2.5$, $P > 0.1$, interaction between coefficient and fROI $F_{3,13} = 1.18$, $P = 0.35$]. For VG, the strength of the covariation was reliably lower overall when response entropy was partialled out (4C *vs.* 4D) [main effect of coefficient $F_{1,15} = 5.944$, $P_{G\text{-}G} < 0.03$, interaction between coefficient and fROI $F_{5,11} = 1.299$, $P = 0.332$].

4. General discussion

The relation between language processing and the cognitive control of thought and action is a widely debated issue in cognitive neuroscience, not least because both faculties encompass unique aspects of human behavior. Within current debates on the level of separability *vs.* integration between language and cognitive control systems in the brain (Fedorenko et al., 2011, 2014; Fedorenko, 2014), the present study contributes new evidence that brain regions included in putatively language-specific brain structures also support key functions of cognitive control, namely the top-down retrieval and selection of (lexico-)semantic representations amongst competing alternatives. It also shows that this network operates in parallel with multiple-demands structures implicated in the maintenance of information in verbal working memory. These findings promote an integrated perspective on the neurocognitive relationship between language processing and cognitive control, contrasting with more radical notions of language and cognitive control as entirely separate processing modules. We discuss these findings and their implications below.

First, our results confirm previous research attributing a key role in the cognitive control of (lexico-)semantic memory to ventrolateral prefrontal (vLPFC) and posterior middle temporal cortices (pMTG) (Badre et al., 2005; Jefferies and Lambon Ralph, 2006; Lau et al., 2008; Whitney et al., 2011; Davey et al., 2016). These regions have recently been described as part of a 'semantic control network' (SCN) recruited in the goal-directed manipulation of semantic knowledge for language and other complex behaviors (Lambon Ralph et al., 2017). Evaluating this proposal in the more specific context of object naming (ON) and verb generation tasks (VG), we show that pMTG and vLPFC support complementary sub-functions of (lexico-)semantic control as depending on task-related demands for selection with or without top-down information retrieval. Specifically, pMTG, the prime candidate region for (lexico-) semantic storage and access (Lau et al., 2008), is predictably not involved in ON insofar as the object displayed is automatically identified through perceptual channels (cf. Etard et al., 2000), while vLPFC remains involved in the selection of names amongst competing alternatives. The same perceptual information, however, is insufficient in VG to access the broad range of verbs conjured up by the same object, leading to more extensive exploration of (lexico-)semantic memory. This additional requirement for top-down (lexico-)semantic retrieval besides information selection explains the joint involvement of pMTG and vLPFC observed in VG.

Second, the covariations observed between BOLD signal change and response entropy in vLPFC and pMTG after partialling out production latencies strongly suggest that (lexico-)semantic retrieval and selection within SCN operate independently from task-related cognitive demands. This observation is consistent with earlier research suggesting that control processes of information selection can be dissociated from general cognitive effort (Koechlin et al., 2003; Christoff et al., 2009; Bourguignon et al., 2018). Our findings, along with previous imaging evidence on working memory (Braver et al., 1997), rather indicate that cognitive effort mainly affects the neural dynamics of the working memory network (WMN) in terms of the amount of information to be considered for selection. Quite interestingly, while the present findings rule out an effect of response entropy as a reliable predictor of the neural dynamics of WMN, they nevertheless point to a causal effect of task differences in selection competition on the association between WMN activity and cognitive effort as reflected in production latencies. As explained previously, the number of alternative responses available for any one trial in VG is substantially greater than in ON (Kurland et al., 2014; Bourguignon et al., 2018). This higher level of competition between candidate responses for each individual trial naturally exerts higher demands for the monitoring of all candidate responses in working memory (Gabrieli et al., 1998; Nagel et al., 2008). Accordingly, though response entropy can be shown to directly capture control demands for information selection (see paragraph above), it can also be shown to influence the degree to which WMN is involved in maintaining the information available for selection.

These and earlier findings (e.g. Geranmayeh et al., 2014; Bourguignon et al., 2018) also show that most regions within the cingulo-opercular network (CON) participate in the cognitive control of language production, though this involvement appears to straddle multiple levels of information integration. Some CON structures can reasonably be assumed to intervene at the motoric level of speech, such as the ventral and dorsal premotor cortex for articulation and anterior cingulate cortex for speech initiation. At the same time, the effect of response competition in modulating their covariation with production latencies also suggests that these same structures may also contribute to the monitoring of information in working memory. Following recent proposals (Postle, 2006), one way to interpret their role as part of the working memory component is in terms of the maintenance of candidate responses through covert articulatory rehearsal. This hypothesis has intuitive appeal as the motor structures involved in executing final verbal responses are also taken to participate in the monitoring of their competitors. The contribution of other CON regions is even more puzzling, as they seem to lie at the nexus between (lexico-)semantic selection, motor control and working memory. The anterior insula, for example, was reliably active in ON and VG but covaried with response entropy only during VG. The functions of the insular cortex in language and behavior have been particularly difficult to elucidate (Oh et al., 2014). Its intricate connectivity patterns with low-level sensorimotor and higher-order cognitive processing networks corroborate its presumed multiplex role in different aspects of human behavior (Cauda et al., 2011). In the present case, we therefore speculate that the insular cortex – perhaps CON as a whole – may provide an interface necessary for the transfer of control signals across motor, (lexico-)semantic and working memory networks.

Our results have general implications for future research on the neurocognitive bases of both cognitive control and language processing. On the one hand, they bolster arguments that cognitive control does not originate from a single brain area or network, but from distributed neural assemblies involved in processing different types of behaviorally relevant information (Petrides, 2005; Badre and D'Esposito, 2009; Dosenbach et al., 2007, 2008; Lambon Ralph et al., 2017). This distributed perspective on cognitive control is featured in several critiques undermining the existence of a central 'controller' to favor the notion of cognitive control as an emergent property of networks geared towards different aspects of action, perception and cognition (Eisenreich et al., 2017, see also Postle, 2006). What differentiates controlled *vs.* automatic modes of information processing within these networks remains to be determined, though available evidence suggests that they depend on separate regimes of oscillatory coherence between their different parts (Buschman and Miller, 2007). This yields the interesting prediction that variations in task demands for controlled (lexico-)semantic processing should be reflected in distinct regimes of neural oscillation in different portions of SCN, inviting closer examination of the range of electrophysiological signatures reflecting controlled *vs.* automatic language processing (Edwards et al., 2010).

On the other hand, our findings underpin a number of grey areas regarding the specificity-generality divide through which linguistically relevant components of cognition have been conceptualized: Among these is the question why verbal working memory, as a language-relevant component, falls within the purview of the brain's general cognitive functions while controlled semantic processing, whose cognitive relevance by several accounts far exceeds language processing (Badre and Wagner, 2007; Lambon-Ralph et al., 2017, Patterson et al., 2007), ought to be considered language-specific. Adjudicating between language-specific *vs.* domain-general processing networks in the brain so far seems to have been based on somewhat arbitrary criteria, and the possibility remains that (parts of) the language network may be involved in processing semantic information in a non-verbal format (Vandenberghe et al., 1996; Corbett et al., 2009). Future efforts should aim at establishing clearer criterial bases on which the distinction between specialized *vs.* peripheral aspects of language processing in the brain can be investigated.

Finally, this research highlights the utility of quantitative notions of cognitive control such as those derived from information theory (Berlyne, 1957; Koechlin and Summerfield, 2007) in tracing the neurocognitive substrates of controlled language processing. Of particular relevance here is that these quantitative measures seem applicable to many different forms of behavior, including spatial navigation (Yoshida and Ishii, 2006), the temporal and hierarchical organization of action (Koechlin et al., 2003) and language production (Bourguignon et al., 2018) and therefore provide a common quantitative workspace within which similarities and differences between the cognitive control of language and other forms of behavior can be investigated. The present research, along with previous efforts to integrate issues pertaining to the study of language production and cognitive control (Levelt, 1989; Novick et al., 2010; Bohland and Guenther, 2006; Nozari et al., 2011), puts the finger on a higher degree of interweaving between these seemingly separate components of human behavior.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.02.043.

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