Recruitment of representational components of the semantic system distinguishes successful from unsuccessful access to complex factual knowledge

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Our ability to effectively retrieve complex semantic knowledge meaningfully impacts our daily lives, yet the interactions between semantic control and semantic representational systems that underly successful access and transient failures in access remain only partially understood. In this fMRI study, we contrast activation during successful semantic access, unsuccessful semantic access due to transient access-failures (i.e., 'tip-of-the-tongue', 'feeling-of-knowing'), and trials where the semantic knowledge was not possessed. Twenty-four participants were presented 240 trivia-based questions relating to person, place, object or scholastic knowledge-domains. Whole brain analyses of the recall event indicate comparable recruitment of prefrontal semantic control systems during successful and unsuccessful semantic access and greater activation in representational systems in successful access. Region-of-interest analysis of domain-selective areas showed that successful access was generally associated with increased responses for both preferred and non-preferred stimuli, with the exception of place-selective regions (PPA, TOS and RSC). Both whole brain and Region-of-interest analysis showed the particular recruitment of place-selective regions during unsuccessful attempts at semantic access, for all stimulus domains. Collectively, these results suggest that prefrontal semantic control systems and classical spatial-knowledge-selective regions work together to locate relevant information and that access to complex knowledge results in a broadening of semantic representation to include regions selective for other knowledge domains.

One of the defining characteristics of the human experience is our ability to learn and retrieve a broad range of complex factual knowledge. Our ability to access this stored semantic knowledge impacts our ability to perform, scholastically, professionally and interpersonally in our daily lives. Yet, the cortical processes underlying this capacity, and the mechanism underlying transient failures in our ability to access this knowledge, remain partially understood.

While we can find ourselves in a situation where we can successfully access a piece of knowledge, for instance, 'what is the capital of Hungary?', we can also find ourselves certain we know the answer but unable to retrieve it, only to be able to do so minutes, hours or days later. Unsuccessful semantic access (also called 'blocking'; Schacter 1999) can be operationally characterised as a temporary failure in access, accompanied by accurate prediction of one's capacity to recall the knowledge in a future test. Subjectively, this can be represented in the common experience of searching through our memory, navigating from related fact to related fact, in an attempt to get closer to the illusive piece of knowledge. Such states can be accompanied by an acute sensation that successful semantic

access is imminent but just out of grasp, the so-called tip-of-the-tongue (ToT) state (Brown and McNeil, 1966, Schwartz, 2002), or the feeling that the knowledge is possessed without the accompanying sense of imminent retrieval (feeling-of-knowing; FoK; (Hart, 1967). These transient failures in access may manifest in the processes that guide semantic access to the appropriate representation or in a failure to ignite that semantic representation itself.

The semantic system includes a left-lateralised set of brain regions that reliably activate more strongly to semantically richer stimuli (Binder et al. 2009). This system has been broadly divided into components thought to control the retrieval of relevant information and brain regions which represent that information. Semantic control regions guide the selection and retrieval of information relevant to the current goal or context (Thompson-Schill et al. 1997; Lambon-Ralph et al. 2017). Due to its involvement in selecting between multiple competing semantic responses, and in making infrequent semantic associations, the left lateral prefrontal cortex (latPFC) is believed to be a key element in semantic control system (Thompson-Schill et al. 1997; Martin and Chao 2001; Wagner et al. 2001; Badre et al. 2005). Additional evidence suggests that semantic control operations in latPFC are supported by a posterior section of the dorsomedial prefrontal cortex, anatomically overlapping with the supplementary motor cortex (dmPFC-SMA), as well as the posterior middle temporal gyrus (pMTG; Whitney et al. 2011; pMTG; Lambon-Ralph et al. 2017; Jackson 2021).

Other components of the semantic system fall within the default-mode network (DMN; Binder et al. 2009), a network of functionally coupled regions generally more active during rest periods and deactivated during cognition that requires cognitive control (Buckner et al. 2008). These regions are candidate components of the representational system and include the precuneus, the angular gyrus, lateral middle temporal gyrus and anterior aspects of the lateral ventral temporal cortex. These area show not only a stronger response to semantically richer stimuli but also multivariate sensitivity to the semantic content of single words (Bruffaerts et al. 2013; Devereux et al. 2013; Fairhall and Caramazza 2013a; Liuzzi et al. 2015, 2020). These regions may work in tandem with neural populations outside this network that encode sensory and modality relevant information (Tyler and Moss 2001; Patterson et al. 2007; Lambon-Ralph et al. 2017) and multiple regions within the brain show selective variation in response amplitude during semantic access to different categories of knowledge (e.g. motor-, tool-, person- or place-related knowledge; Hauk et al. 2004; Noppeney et al. 2006; Fairhall and Caramazza 2013b; Fairhall et al. 2014; Fernandino et al. 2015; Fairhall 2020). Notably, this selectivity is particularly evident for more complex sentence-level stimuli referencing different knowledge domains (Rabini et al. 2021).

These control and representational components of the semantic system work hand-in-glove to allow successful semantic access and transient failures in either or both subsystems may differentiate successful from unsuccessful access. Previous neuroimaging work investigating unsuccessful access has highlighted the semantic control system. Increased activation of prefrontal control systems in both hemispheres is evident when comparing unsuccessful access to a combination of successful and knowledge-absent trials

(Maril et al. 2001, 2005) or when parametrically comparing unsuccessful semantic access trials and trials where the fact is unknown (Kikyo et al. 2002). Identified prefrontal regions include both those implicated in semantic cognition (left IFG, dlPFC-SMA) as well as those that are not (right IFG, bilateral anterior PFC). Moreover, the recruitment of these regions occurs in a graduated manner, with greater cortical responses for ToT than FoK states (Maril et al. 2005). One potential consideration is that studies that have compared known to blocked states have included in the modelled fMRI response both the recall-event and the subsequent metacognitive evaluation of the participants internal cognitive state during recall-event. Consequently, the involvement of frontal regions may reflect extra-semantic processes such as response selection of cognitive conflict associated with the metacognitive judgement (Maril et al. 2005).

The objective of the current study is to gain insight both into the processes underlying temporary blocks in semantic access and those that allow successful access to stored knowledge. We contrast the fMRI response associated with successful semantic access, unsuccessful semantic access and trials where semantic knowledge is absent. This study extends the extant literature in two ways. Firstly, we employ an fMRI design that permits the deconvolution of the cortical responses to the cognitive recall-event from subsequent metacognitive decisions about the degree of confidence that the knowledge is possessed. Secondly, we further examine the role of representational components of the semantic system in successful and unsuccessful semantic access. To accomplish this, we employ general knowledge questions drawn from four different knowledge domains: relating to people, places, objects and to a category we term scholastic, which is designed to focus on facts which are derived verbally and are less likely to be drawn from environmental experience or relate to particular object classes. This manipulation of the semantic content of the probe stimuli allowed us to better isolate regions involved in representational processes as well as to understand the relationship between knowledge-domain selectivity in the cortex and successful and unsuccessful semantic access. This approach additionally allowed us to identify neural processes associated with the search for possessed knowledge ([successful≈unsuccessful] > knowledge-absent) and those involved in access to the relevant piece of factual information (successful > unsuccessful). We found that the internal search for the relevant factual knowledge recruited both prefrontal semantic control systems and regions implicated in place-knowledge, and that successful and unsuccessful access are distinguished by the broad recruitment of semantic representational systems.

MATERIALS AND METHODS

Participants

Twenty-nine right-handed native-Italian speakers with no history of neurological disorder were recruited for the study. Three participants were excluded due to within-run head motion exceeding 2 mm or excessive ocular artifacts during scanning. One subject was excluded as they did not report any of the place or scholastic facts to be unknown and a further participant did not complete the entire experiment. Thus, the final sample included

24 participants (10 males, mean age 26.4 years). Participants gave informed consent and were compensated for participation (15 €/hour). The study was conducted in line with the declaration of Helsinki (1964, amended in 2013) and was approved by the Ethics Committee at the University of Trento.

Experimental Design

Stimuli. Stimuli were composed of 240 Italian written general-knowledge questions. The questions were equally divided into four knowledge domains: People, in which there were questions about famous historic or fantasy characters or famous contemporary people (e.g. '*Which philosopher uttered the phrase I know I dont know?*'); Places, where they were asked about famous geographic places or monuments (e.g. *'In which Spanish city is the Alhambra complex located?'*); Objects, in which the questions were about specific objects or materials (e.g. *'What is the name of the element that supports the weight of an arch?'*) and Scholastic, where participants were asked about abstract topics studied in school (e.g. *'What is the name of the transition of matter from the solid to the gaseous state?'*). Stimuli were matched across knowledge-domain by number of words ($F_{(3,236)}$=1.13, p=.337) and number of letters ($F_{(3,236)}$=1.12, p=.343). The full list of stimuli is available as supplementary material (table S1).

fMRI Experimental Task. The fMRI session was divided into 4 experimental runs. In each run, fifteen questions from each knowledge-domain were presented in a pseudo-randomized order using Matlab (www.mathworks.com) and Psychtoolbox Version 3 (www.psychtoolbox.org). Each trial was divided into two parts. Firstly, the recall-event included the 3-second written presentation of the question followed by a 3-second fixation cross. Participants indicated via button press whether the knowledge was accessible or inaccessible (non-responses (<1%) were coded as inaccessible). If participants indicated they could access the answer, the experiment continued to the next trial. Inaccessible response prompted a 0 to 8 seconds jitter followed by a metacognitive judgement. Here, participants were cued to indicate whether they experienced a TOT, a FOK, or that they answer was unknown (4 second duration).

Post Scanner Knowledge-Verification Test. To validate the self-reported responses in the scanner, after the fMRI session participants were again presented with the questions classified as ToT, FoK or unknown, as well as 20% of the 'known' questions. Participants were allowed 5 seconds to type the answer to each question without any cue. If the participant did not respond or the participant opted to proceed to the cue (via button press), the first letter of the answer appeared, and they had an additionally 5 seconds to start typing the response.

MRI scanning parameters

Functional and structural data were collected at the Center for Mind/Brain Sciences (CIMeC), University of Trento, with a Prisma 3T scanner (Siemens AG, Erlangen, Germany), using a 64-channel head coil. Participants lay in the scanner and viewed the visual stimuli through a mirror system connected to a 42", MR-compatible, Nordic NeuroLab LCD monitor positioned at the back of the magnet bore. Functional images were acquired using echo planar (EPI) T2*-weighted scans. Acquisition parameters were: repetition time (TR) of 2 s, an echo time (TE) of 28 ms, a flip angle of 75°, a field of view (FoV) of 100 mm, and a matrix size of 100 x 100. Each volume consisted of 78 axial slices (which covered the whole brain) with a thickness of 2 mm, AC/PC aligned. High-resolution (1×1×1 mm) T1-weighted MPRAGE sequences were also collected (sagittal slice orientation, centric phase encoding, image matrix = 288 × 288, field of view = 288 mm, 208 slices with 1-mm thickness, repetition time = 2290, echo time = 2.74, TI = 950 ms, 12° flip angle).

fMRI Data Analysis

Data were analysed and preprocessed with SPM12 (http://www.fil.ion.ucl.ac.uk/spm/). The first 4 volumes of each run were dummy scans. All images were slice-time corrected, realigned to correct for head movement, normalised to MNI space and smoothed using a 6mm FWHM isotropic kernel. Before computing the General Linear Model, the four runs were concatenated, to avoid empty parameters in one or more conditions. Sixteen trial types were modelled for the recall event: the four different access-types (successful-access, ToT, FoK and knowledge-absent trials) for each of the four knowledge domains. An additional twelve conditions for the metacognitive part of the trials, with TOT, FOK and knowledge-absent responses modelled for each of the four categories. Subject-specific parameter estimates (β weights) for each of these 28 conditions were derived through the GLM. The 6 head-motion parameters were included as additional regressors of no interest. Group level analysis was performed in two separate random effects GLMs, one for the recall event and one for the metacognitive judgment.

A region-of-interest (ROI) analysis was performed to assess the effect of access type within knowledge-domain-selective brain regions. ROIs were defined via the orthogonal domain-selective contrasts (e.g. place > mean(person, object, scholastic)) and are therefore unbiased with respect to the influence of access type. For each of the four knowledge domains, ROIs were constructed by taking the union between a sphere with a radius of 5mm centred at the selectivity peak for the knowledge-domain (see table 2) and statistically significant voxels for the relevant domain-selective contrast (see figure 3).

Results

Behavioural

Participants reported that the fact was known on 45.6% of trials, ToT states on 12.7% of trials, FoK states on 16.3%, and that the fact was unknown on 25.5%, in keeping with previous results using similar paradigms (Maril et al. 2001, 2005). Post-scanner testing indicated that known responses were genuine, with 79.5% of correct responses being

correctly provided, either through free recall (48.8%) or when cued by the first letter of the word (30.8%). Participants were able to subsequently recall the correct answer for 60.0% of tip of the tongue responses (32.3% unprompted, 27.2% cued) and 38.0% of FoK responses (16.9% unprompted, 21.1% cued). Subjects could accurately report 20.4% or unknown responses (8% unprompted, 11.9% cued).

Repeated measure ANOVA revealed that response type differed across knowledge-domain ($F_{(9,207)}$=6.20,p<.001). While the number of known responses did not differ significantly across domains, ToTs were less frequent for person (10.9%) and place domains (11.0%) compared to both object (14.9%) and scholastic domains (14.1%; p-values: .020-.001). FoKs were less likely in the person domain (12.2%) compared to place (18.2%), object (16.4%) and scholastic (18.4%) domains. These effects were balanced by an increase in confirmed unknown responses for people (33.5%) and place (27.9%) domains compared to object (22.0%) and scholastic (18.4%) domains.

To assess RTs for the initial access event, the responses were decomposed based on the subsequent metacognitive judgment. The effects of response type (known, ToT, FoK and knowledge-absent) and knowledge domain (people, places, objects and scholastic) were then assessed via repeated measures ANOVA. RTs differed as a function of response type ($F_{(3,69)}$=41.6, p<.001). Paired t-test revealed that ToT (3797 msec) and FoK (3730 msec) did not significantly differ ($t_{(23)}$=1.57, p=.13) and were slower than responses subsequently confirmed to be unknown (3464 msec; v. ToT $t_{(23)}$=5.43, p<.001; v. FoK $t_{(23)}$=5.08, p<.001). Unknown responses were in turn slower than known responses (3238 msec; $t_{(23)}$=4.97, p<.001). RTs also differed as a function of knowledge domain ($F_{(3,69)}$=28.3, p<.001). Judgments for people trials (3361 msec) were faster than for places (3548 msec; $t_{(23)}$=4.31, p<.001), which were in turn faster than objects (3670 msec; $t_{(23)}$=3.49, p=.002) and scholastic items (3651 msec, $t_{(23)}$=2.84, p=.009), which did not differ significantly from one another ($t_{(23)}$=0.64, p=.53). There was no interaction between response type and knowledge domain ($F_{(9,207)}$=.99, p=.45).

RTs for the metacognitive judgment differed modestly as a function of category ($F_{(3,69)}$=2.88, p=.042), with faster responses for people (559 msec) than for objects (618 msec, $t_{(23)}$=2.42, p=.024) and scholastic (604 msec, $t_{(23)}$=2.46, p=.022) domains. Response type had a more pronounced influence on RTs ($F_{(2,46)}$=10.63, p<.001), with slower responses for FoK (673 msec) compared to both ToT (569 msec, $t_{(23)}$=3.59, p=.002) and unknown (560 msec, $t_{(23)}$=5.90, p=.001) responses.

Inclusive Masking

Unexpectedly, known responses were associated with the strong activation of striatal and orbitofrontal regions associated with reward (see also, Kikyo et al. 2002). To focus analyses on regions involved in semantic processing, subsequent analyses have been restricted to regions showing sensitivity to semantic category at an uncorrected (p<.05) threshold (omnibus ANOVA: main effect of category, see figure 1). At this lenient threshold, the mask can be seen to encompass both control and representational aspects of the semantic

system. In contrast, examination of excluded regions showing a stronger response for successful access trials with Neurosynth image decoder (https://neurosynth.org/decode/; Yarkoni et al. 2011; Rubin et al. 2017), indicated correspondence with reward circuitry (prob.=.387, the highest non-anatomic reverse-inference term).

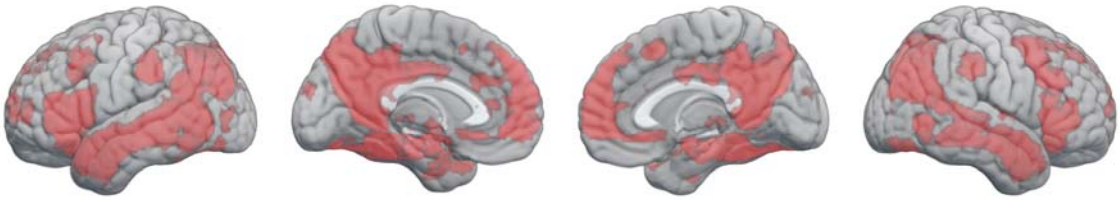

Figure 1. *Inclusive functional mask applied to all contrasts in this study. The mask was defined as regions showing sensitivity to knowledge-domain at a lenient statistical threshold (p<05, uncorrected).*

Neural correlated of blocked and successful semantic access

Within the inclusive mask, we first compared unsuccessful retrieval (ToT/FoK) to trials where the knowledge was absent (figure 2 and table 1). Relative to knowledge-absent trials, unsuccessful access recruited semantic control circuitry in the left lateral prefrontal cortex and medial supplementary motor cortex. Additionally, the bilateral retrosplenial complex (RSC), left parahippocampal gyrus, the transverse occipital sulcus, and a region of the supramarginal gyrus, were more active during FoK/ToT than knowledge-absent trials.

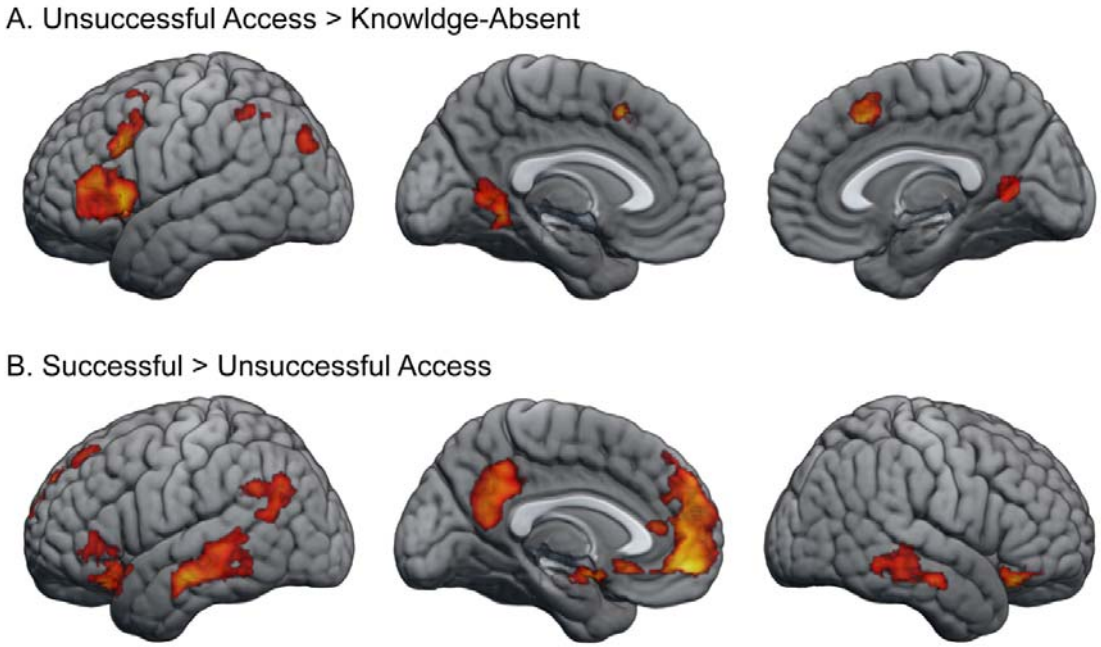

Figure 2. *Successful and unsuccessful access during the recall-event. Shown is the response to A) unsuccessful semantic access compared to trials where the knowledge was absent (ToT and FoK trials > knowledge-absent trials) and B) Successful > Unsuccessful access. Brain maps show the response during the recall event, when participants indicated whether the*

knowledge was accessible or inaccessible (with inaccessible responses coded into ToT, FoK or knowledge-absent trials based on the subsequent metacognitive judgement). Brain maps were thresholded with an initial voxel-wise threshold of p<.001 and cluster corrected at p<.05. See table 1 for significance, extent and location of clusters.

To delineate the neural processes associated with successful semantic access from failed semantic access, we contrasted successful to unsuccessful (ToT/FoK) access. Results show increased cortical activity in a network of regions associated with the representation of semantic knowledge: the precuneus, mPFC, bilateral sections of the middle temporal gyrus and the left angular gyrus and hippocampus. Additionally, lateral orbitofrontal cortex in both hemispheres were seen to be more active when stored information was successfully accessed. Notably, activation in the left OFC was seen to extended laterally into the pars triangularis of the IFG

No regions showed a significant difference between ToT and FoK trials during the recall event (but see later section: metacognitive judgements of knowledge confidence).

Table 1. *Significance, extent and location of regions showing differential responses for successful and unsuccessful semantic access as shown in figure 2. For large clusters spanning multiple regions, local maxima are listed separately.*

Abbreviations

		cluster p(FWE-corr)	cluster equivk	peak T	x,y,z {mm}
Unsuccessful Access > Knowledge-Absent	**IFG (opercular)**	<.001	1071	6.98	-34 20 -4
	IFG (triangular)			5.29	-44 30 12
	dmPFC-SMA	.001	227	6.22	4 20 44
	left post. PHG	<.001	627	5.74	-20 -50 -6
	right RSC			4.79	18 -56 10
	left RSC			4.01	-8 -56 2
	left premotor	<.001	342	5.38	-44 16 34
	MFG	.010	140	4.53	-28 10 50
	inf parietal	.003	172	4.32	-32 -58 38
	left TOS	.008	144	4.07	
					-34 -82 30
Successful Access > Unsuccessful Access	**vmPFC**	<.001	2732	6.48	-4 48 -10
	medial OFC			6.05	6 18 -12
	right OFC	<.001	354	6.38	30 38 -18
	left hipp	<.001	645	6.16	-12 6 -14
	left OFC			5.10	-34 26 -22
	left MTG	<.001	942	5.21	-58 -18 -16
	precuneus	<.001	1042	5.03	-2 -56 22
	left AG	<.001	419	4.53	-48 -66 28
	right mid MTG	<.001	409	4.43	64 -16 -18

Abbreviations. IFG: inferior frontal gyrus; dmPFC-SMA: dorsomedial PFC - supplementary motor area; PHG: parahippocampal gyrus; RSC: retrosplenial cortex; TOS: transverse occipital sulcus; MFG: middle frontal gyrus; vmPFC: ventromedial PFC; hipp: hippocampus; OFC; orbitofrontal cortex; inf: inferior; post: posterior.

Comparing unsuccessful to successful semantic access

The contrast of unsuccessful > successful access identified two small clusters. One in the left premotor area in a region overlapping with the frontal eye-fields (extent: 174 voxels; p_{corr}=.003; xyz_{MNI}: -22 -2 52) and another in the left superior parietal lobe (extent: 163 voxels; p_{corr}=.004; xyz_{MNI}: -8 -72 52). Follow up investigation showed that these regions were not more responsive for unsuccessful access compared to knowledge-absent trials and the nature of this effect remains ambiguous.

Knowledge-domain-selective responses

To identify brain regions sensitive to semantic content, each knowledge domain was contrasted to the average of the other three knowledge domains. Knowledge-domain selectivity was evident in an extensive set of temporal, parietal and prefrontal regions (Figure 3, Table 2). Person knowledge selectively activated bilaterally: mid and anterior middle temporal gyrus, angular gyrus, premotor cortex and hippocampi; medially: the precuneus and mPFC; as well as the lateral fusiform gyrus in the right hemisphere. In addition to the classic place-selective network, (PPA, RSC, TOS) place stimuli more strongly recruited superior aspects of the prefrontal cortex bilaterally, left pMTG and the midcingulate cortex. Notably, three regions outside of the semantic control network which show an increased response during blocked semantic access (figure 2A), correspond to left PPA and TOS and bilateral RSC. Object-related retrieval events selectively activated bilateral IFG, pMTG and lateral fusiform gyri as well as the left supramarginal gyrus and perirhinal cortex. Scholastic retrieval events selectively activated left IFG and the posterior superior temporal sulcus bilaterally. The degree of overlap in voxels showing a preference for more than one domain (indicated by blended colourmaps in figure 3) was minimal.

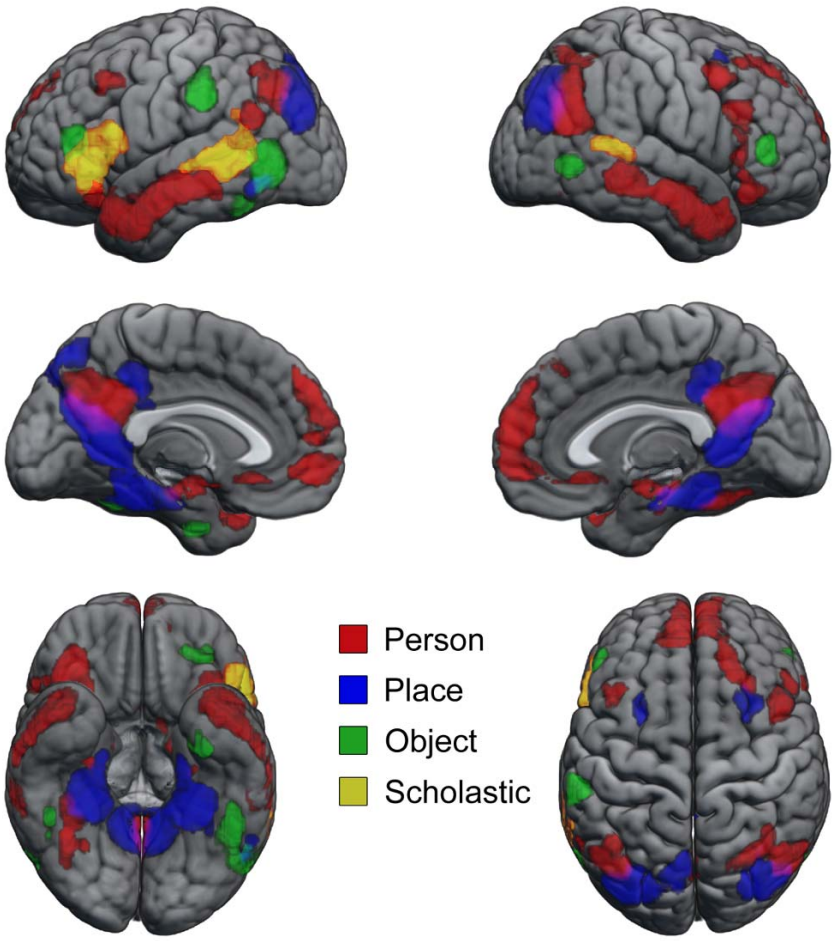

Figure 3. *Cortical regions demonstrating a preference for one category versus the average of the others during the recall attempt, irrespective of recall outcome. Brain maps are initially thresholded at a voxel-wise threshold of p<.001 and cluster-level corrected* p_{FWE}*<.05.* See table 2 for significance, extent and location of clusters.

Table 2. *Significance, extent and location of regions showing differential responses for knowledge domain, as shown in figure 3. For large clusters spanning multiple regions, local maxima are listed separately. Italicised regions are incorporated in subsequent ROI analyses.*

		cluster $p_{(FWE\text{-}corr)}$	voxels	peak T	x,y,z {mm}
Person	***Precuneus***	<.001	2127	11.77	4 -54 26
	right mid MTG	<.001	2111	11.67	-60 -14 -16
	right ant. MTG			7.36	-48 8 -30
	left mid MTG	<.001	1700	10.28	58 -10 -16
	left ant. MTG			8.46	42 12 -34
	right AG	<.001	1664	9.98	52 -68 26
	vmPFC	<.001	2345	9.34	-6 56 -14
	mPFC			7.69	-8 54 40
	right OFC	<.001	556	8.13	34 34 -16
	medial OFC	.011	137	6.55	-4 24 -12
	left hipp	<.001	236	6.08	-20 -10 -16
	right dlPFC	<.001	336	5.93	44 20 26
	right hipp	<.001	268	5.91	20 -8 -14

	right FG	<.001	341	5.78	38 -38 -24
	left AG	<.001	998	5.71	-38 -70 42
	right dlPFC	<.001	280	4.97	46 10 48
	left dlPFC	.001	195	4.47	-38 14 42
Place	***right RSC***	<.001	6881	22.33	14 -54 16
	left RSC			21.22	-14 -60 20
	left PPA			16.8	-28 -42 -10
	left TOS			13.25	-36 -82 -10
	right PPA	<.001	1090	12.95	28 -34 -18
	right TOS	<.001	1299	11.86	38 -76 36
	mid cingulate	<.001	618	8.2	-4 -36 40
	left premotor	<.001	374	7.47	-24 8 50
	right premotor	<.001	418	5.97	26 16 46
	left post. MTG	.034	107	4.81	-54 -62 -10
Object	***left post. MTG***	<.001	1104	9.03	-54 -66 0
	left latFG			7.76	-48 -50 -18
	left IFG	<.001	326	8.03	-44 34 10
	right IFG	<.001	235	7.82	44 38 8
	SMG	<.001	379	7.23	-56 -32 34
	perirhinal	.015	129	6.26	-32 -10 -38
	left OFC	.028	112	7.75	-30 38 -8
	right latFG	<.001	299	5.06	48 -44 -18
	right post. MTG			5.03	54 -66 0
Scholastic	***left IFG***	<.001	872	6.52	-52 26 2
	left MTG	<.001	1050	6.51	-64 -50 4
	right MTG	<.001	502	5.14	58 -38 8

Abbreviations: MTG: middle temporal gyrus; AG: angular gyrus; mPFC/vmPFC/dlPFC; medial/ventromedial/dorsolateral PFC; OFC; orbitofrontal cortex; RSC: retrosplenial cortex; PPA: parahippocampal places area; TOS: transverse occipital sulcus; latFG: lateral fusiform gyrus; SMG: supramarginal gyrus; ant: anterior; post: posterior.

Effect of access-type within domain-selective brain regions

To investigate the influence of recall type within brain regions exhibiting a sensitivity to semantic content, ROIs were defined via the orthogonal domain-selective contrasts presented in figure 3 and table 2). To reduce multiple comparisons over the large number of identified domain-selective regions, analyses were performed by averaging the responses of ROIs within each network. Specifically, the six most strongly selective regions (indicated in italics in table 2) were selected for person, place and object domains and all three regions for the scholastic domain.

Within person, object and scholastic domain-selective networks, an overall increase in activity irrespective of sentence domain was seen from knowledge-absent to successful-access trials (all p-values<.0001) and from unsuccessful access to successful access trials (all p-values<.005; see figure 4A). Increased activation during unsuccessful access compared to knowledge-absent trials was largely absent, with modest effects limited to the object-domain-selective network (p=.031). Notably, within these domain-selective networks, the modulation by access-type was not sensitive to stimulus domain. For comparison, figure 4B shows the effect of recall-type for each network's preferred stimulus type and figure 4C shows the response for the average of the three non-preferred stimulus classes. Descriptively, the response profile across different recall-types in person, object and scholastic domain-selective networks can be seen to be largely similar for preferred and non-preferred stimulus classes. Weighted contrasts confirmed that the increase from knowledge-absent to successful-access trials did not differ between the preferred domain seen in figure 4B and the average of the non-preferred domains seen in figure 4C (all p-values >.21) and increases from unknown to known trials were evident when only the non-preferred categories were considered (p-values <.005; figure 4C). This indicates that, in person, object and scholastic domain-knowledge-selective regions, the enhanced response associated with successful access was not domain-selective.

A different profile was evident within the place-selective network. Like the other domain-selective networks, a domain-general increase was present from unknown to known trials (p<.0001). Unlike the other networks, the increased response from knowledge-absent to successful-access trials was domain selective. Specifically, there was a greater increase for place-related trials compared to the other domains (p=.002) and there was no significant increase from unknown to known trials when only the three non-preferred categories were considered (p=.1). In addition, place selective regions exhibited a robust increase in response for unsuccessful-access trials relative to knowledge-absent trials (p=.0002), an effect that persisted when only non-preferred stimuli were considered (p=.004). This indicates that place-selective regions, the PPA, RSC and TOS, are recruited during the attempts to access semantic knowledge and that this is true not only for place-related information but for all knowledge-domains.

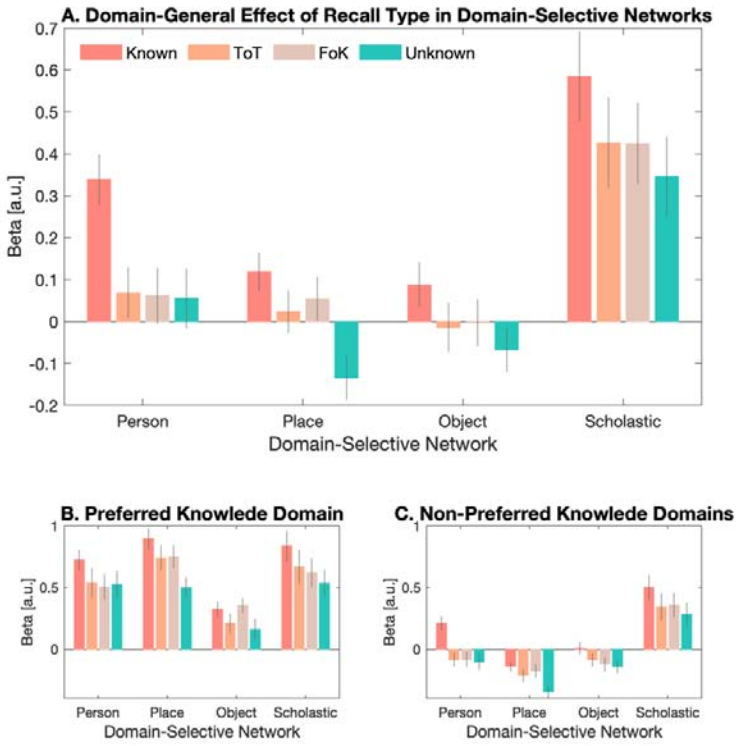

Figure 4. *Effect of Recall Type within Knowledge-Domain-Selective Cortical Networks.* ***A.*** *Effect of Recall Type for all stimulus domains.* ***B****. Effect of Recall Type for each network's preferred domain (e.g., person-related questions in person-selective regions).* ***C.*** *Effect of Recall type for each network's non-preferred domain (e.g., the average of place-, object-, scholastic-related questions in person-selective regions). Error bars indicate 1 standard error of the mean.*

Metacognitive judgments of knowledge confidence

To examine the neural correlates associated with the metacognitive judgement of the degree of confidence with which inaccessible knowledge was believed to be possessed, we compared ToTs and FoKs to unknown responses in the metacognitive stage of the trial. Both ToTs and FoKs activated prefrontal control regions bilaterally and medially (see figure 5). There was a graduated response, with greater responses for ToTs than FoKs. Specifically, all regions showing a response to FoKs also exhibited a response to ToTs. Activation of control circuitry was more expansive for ToTs than FoKs and was significantly stronger in bilateral IFG and the right middle frontal gyrus. ToTs additionally activated representational components of the semantic system the mid lateral MTG bilaterally and the left temporoparietal junction.

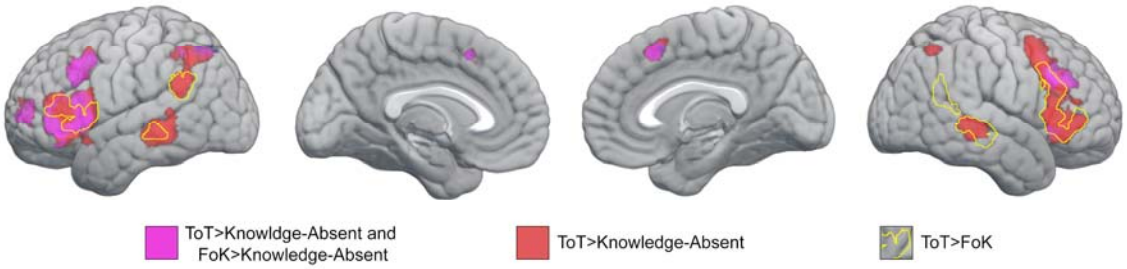

Figure 5. *Whole-brain analysis of metacogntivie judgment comparing ToT, FoK and knoweldge-absent responses. Brain maps are initially thresholded at a voxel-wise threshold of p<.001 and cluster-level corrected p_{FWE}<.05. See table 3 for significance, extent and location of clusters.*

Table 3. *Significance, extent and location of regions during the recall event as shown in figure 5. For large clusters spanning multiple regions, local maxima are listed separately.*

	ToT > Knowledge-Absent				*FoK > Knowledge-Absent*				*Tot>FoK*			
	cluster		peak		cluster		peak		cluster		peak	
	$p_{(FWE\text{-}corr)}$	voxels	T	x,y,z {mm}	$p_{(FWE\text{-}corr)}$	voxels	T	x,y,z {mm}	$p_{(FWE\text{-}corr)}$	voxels	T	x,y,z {mm}
IFG	<.001	2027	8.69	-50 18 0	<.001	1099	5.07	-52 16 4	<.001	530	4.58	-50 18 0
ant. IFG			7.2	-44 42 -4			5.84	-44 42 0				
dmPFC-SMA	.001	191	6.8	2 26 46	.003	165	5.93	-4 18 50				
ant. PFC	.017	120	7.05	-40 52 4	.027	109	5.09	-32 60 6				
left premotor	<.001	610	6.9	-42 10 38	<.001	469	5.69	-38 8 42				
right MFG	<.001	2193	6.73	46 22 32	<.001	288	4.93	44 40 28				
right IFG			6.41	40 24 -8	.022	114	5.03	40 24 -8	<.001	586	4.49	42 40 2
Left IPS	<.001	1297	6.68	-48 -48 48	<.001	784	5.87	-26 -56 38				
right mid MTG	<.001	628	6.75	46 -30 -2					<.001	443	5.81	54 -28 -2
left mid MTG	<.001	855	6.13	-60 -36 -6					.003	163	4.27	-58 -34 -6
right IPS	.014	125	4	44 -60 52								
cerebellum	.002	173	6.35	-32 -62 -32								
cerebellum	.044	97	6.82	-8 -78 -30								
left TPJ									.004	161	4.18	-54 -44 32
right TPJ									.036	102	4.43	60 -54 20

Abbreviations. IFG: inferior frontal gyrus; dmPFC-SMA: dorsomdeial PFC - supplimentary motor area; MFG: middle frontal gyrus; IPS: interaparietal suclus; MTG: middle temporal gyrus; TPJ; temproparietal junction; ant: anterior.

Discussion.

In this work, we examined the neural processes that underly successful and unsuccessful access to stored semantic knowledge – those neural states that characterise our transient inability to access a fact in an exam or conversation and those states which result in our successful ability to do so. Using this paradigm, we were able to identify neural processes associated with the search for possessed knowledge ([successful≈unsuccessful] > knowledge-absent) and those involved in access to the relevant piece of factual information (successful > unsuccessful). The internal search for factual knowledge was associated with activation of both prefrontal semantic control circuitry and recruitment of cortical regions traditionally associated with place-related processing. Successful access was associated with increased in activation in representational subcomponents of the semantic system. The processing of complex factual information was seen to rely on an extended collection of knowledge domain-selective cortical regions. Examination of recall-type within person, object and scholastic domain-selective subsystems, indicated that the increased activation

associated with successful access was domain-general, being comparably evident for both preferred and non-preferred stimulus classes.

Comparable recruitment of semantic control systems during successful and unsuccessful semantic access.

Relative to knowledge-absent trials, unsuccessful attempts at semantic access resulted in increased activation in semantic control regions: opercular and triangular sections of the IFG, and the dmPFC-SMA. Increased activation of IFG and dmPFC-SMA during unsuccessful semantic access is consistent with a cognitive process where attempts are being made to guide selection towards the illusive semantic representation. It is notable that a third region implicated in semantic control, the pMTG (Jackson et al. 2016; Lambon-Ralph et al. 2017), did not show a modulation during this task. Such findings may potentially reflect a differentiation in semantic control operations occurring in pMTG. Alternatively, this dissociation may reflect the non-absolute nature of the dichotomy between control and representational functions in *pMTG,* which responds selectively for specific semantic classes such as 'tools' (Noppeney et al. 2006) and is sensitive to the semantic distance between concepts (Fairhall and Caramazza 2013a). Place-selective regions, the PPA, RSC and TOS exhibited an increased response during unsuccessful access. These regions are not implicated in the semantic control and their observed recruitment during unsuccessful attempts at semantic information is discussed later in the context of knowledge-domain-selective networks.

In contrast with previous studies, in the moment of recall we did not observe greater activation for unsuccessful than successful access in control systems. Rather we observed generally comparable recruitment of semantic control regions with a restricted area of the orbital region of the left IFG showing greater activation for successful access. This disparity may be partially attributable to the particular statistical comparisons used in previous works. For example, Maril and collegues (2001) compared unsuccessful access to the average response of both knowledge-absent and successful-access trials, while Kikyo and colleagues (2002) used a parametric analysis comparing knowledge-absent trials and different levels of confidence for unsuccessful-access trials and did not directly compare successful to unsuccessful access. It is also possible that differences between previous and the present studies are attributable to the influence of the metacognitive ToT and FoK judgement, which was not separated from the cognitive recall-event in some prior works.

Further recruitment of control systems in the metacognitive judgement was observed in the present study. ToTs and FoK judgment activated prefrontal systems to a greater than knowledge-absent judgements. As in previous work, this occurred in a graded manner with ToTs producing greater responses than FoKs (Maril et al. 2005). Moreover, effects were apparent not only in classically semantic prefrontal regions, the left IFG and dmPFC-SMA, but additionally in frontal regions in the right IFG, MFG and anterior PFC, consistent with previous studies (Maril et al. 2001, 2005). These results allow that previously reported prefrontal recruitment during ToT and FoK states could arise from the

metacognitive component of ToT or FoK state, potentially reflecting additional prefrontal cognitive processes, such as response selection or conflict resolution (Maril et al. 2001, 2005).

Collectively, these results indicate that the recruitment of semantic control systems is largely comparable between successful and unsuccessful semantic access and that the metacognitive components of ToT and FoK judgments contribute to additional prefrontal activations.

Increased recruitment of representational semantic regions differentiates successful from unsuccessful semantic access.

Compared to unsuccessful semantic access, successful access resulted in the increased recruitment in cortical regions associated with semantic representation. Specifically, activation increased in bilateral mid MTG, the left angular gyrus, vmPFC, and the precuneus, regions frequently implicated in semantic representation (Binder et al. 2009; Lambon-Ralph et al. 2017). Additionally, we saw recruitment of the left hippocampus, a region recently implicated in non-control aspects of semantic cognition (Jackson 2021). Finally, we observed increased activation in bilateral OFC. Lateral OFC has been reported to show selective responses for faces when information is accessed about famous people (Aglinskas and Fairhall 2020) and exhibited a preference for the person knowledge-domain in the present study.

Collectively, these results indicate that successful and unsuccessful semantic access are associated with comparable activation of semantic control circuitry and distinguished by a relative failure to ignite semantic representational stores during unsuccessful access. In the next section, we explore this in more detail within ROIs selective for the different knowledge-domains.

Processing of complex factual information relies on knowledge-domain-selective neural substrates.

While often reported for image processing in ventral and dorsal streams, category-selective responses are less common for word stimuli (Bi et al. 2016). Here, using sentences depicting specific semantic categories, we observe robust selectivity for the four utilised knowledge domains extending over temporal, parietal and prefrontal regions. As in previous work, person-selective activation is apparent in the precuneus, mPFC, bilateral TPJ and lateral aspects of the ATL during semantic access (Fairhall and Caramazza 2013b; Fairhall et al. 2014; Rabini et al. 2021). Person-selective activation was also evident in the right lateral fusiform gyrus anatomically overlapping the FFA. This is notable in that selective activation of this region by non-picture stimuli is seldom reported (Bi et al. 2016), although linguistic phrases have been previously shown to activate this region more so than non-linguistic vocalisations or mathematical calculations in the blind (Kanjila et al, 2015, Fairhall et al, 2015). The present result suggests that, while singular individual concepts do not selectively activate these regions, more complex person-related semantic information that links

together multiple concepts, may. Person-selective responses were additionally evident in the hippocampi bilaterally and regions of the lateral PFC.

Access to place-related information preferentially recruited bilateral PPA, RSC and TOS, consistent with the selectivity of these regions during the perception of scenes and access to spatial and geographic knowledge (Epstein et al. 2007; Dilks et al. 2011; Fairhall 2020) and word-cued semantic access to place knowledge (Fairhall and Caramazza 2013b; Fairhall et al. 2014; Bi et al. 2016). In addition, we observed activation of the section of the posterior cingulate cortex immediately anterior to that exhibiting person selectivity. Consistent with previous studies of sentence level stimuli (Rabini et al. 2021) and semantic categorisation judgments of people and places (Fairhall and Caramazza 2013b; Fairhall et al. 2014) we saw place-selective increases in left pMTG. We also observed place-selective responses in bilateral superior sections of the premotor cortex, that have previously been reported in the left hemisphere when reading simple sentence involving places (Rabini et al. 2021).

Facts relating to objects selectively activated the left pMTG, extending into lateral aspects of the left fusiform gyrus. Approximately 44% of object-related facts employed in this study relate in some way to manipulable objects (instruments, sport-related items, tools; see supplementary material 1), which are known to selectively recruit this region when utilising single words depicting manipulable objects (Chao et al. 1999; Noppeney et al. 2006; Peelen et al. 2013; Rabini et al. 2021), or when encoding new information about tools (Simmons et al. 2010). Both pMTG and lateral FG were also present in the right hemisphere but less strongly. In addition, object-related facts selectively activated the supramarginal gyrus, a region, like the pMTG, that has been implicated in object-manipulation knowledge (Fernandino et al. 2015). Notably, as was the case for the person-knowledge domain, object selective activation was associated with cortical regions traditionally implicated in semantic control, bilateral superior aspects of the IFG. Finally, objects preferentially activated ventromedial ATL in a region consistent with the perirhinal cortex, a region showing multivariate sensitivity to the semantic relationship between objects (Bruffaerts et al. 2013; Liuzzi et al. 2015).

The final domain of knowledge, 'scholastic', was designed to capture category-general factual knowledge that was unrelated to direct experience with the environment, more likely to be learned verbally, and did not involve person-, place or object-related information. This form of knowledge selectively activated core regions of the semantic system, either those implicated in control (left IFG) or in semantic representation (left and right mid MTG, in both hemispheres; Lambon-Ralph et al. 2017). Selective recruitment of left IFG is certainly consistent with scholastic information requiring additional control. However, the collective pattern of selectivity across domains also allows another possibility. As noted, not only are lateral prefrontal regions selective for scholastic knowledge, but sections of the left and right IFG are also selective for object and person knowledge-domains. The tiled nature of this selectivity makes it unlikely that this reflects overall differences in demands for semantic control. This pattern may indicate partial

representation of semantic content within these regions or that semantic control systems are anatomically organised into subsystems that interact with different domain-selective semantic representations.

Successful and unsuccessful semantic access in knowledge-domain-selective cortex.

The influence of semantic access in domain-selective regions is complex but informative. In a region of interest analysis, we compared the fMRI response averaged across key elements of networks exhibiting a selective response for person, place, object and scholastic domains of knowledge. ROI results supported the whole-brain analysis. Consistent with the whole brain analysis, robust increases in activation from knowledge-absent to unsuccessful access were seen only in place-selective regions. Likewise, increased activation in knowledge-domain-selective ROIs for successful compared to unsuccessful access mirrored patterns seen in the whole brain analysis, while demonstrating the widespread extent of this effect.

Successfully accessing the specific piece of factual knowledge indicated in the question may result in a focussing of the recruited representations to those knowledge-domain-selective regions most relevant to the piece of knowledge, which would manifest in a relative increase in tuning in relevant knowledge-domain-selective regions. Alternatively, access to the fact may bring with it broader associated memories, relying on representations present in cortical regions both selective for the relevant domain and those selective for other domains. While all networks showed overall increases in activity during successful compared to unsuccessful semantic access, in networks selective for person, object and scholastic knowledge-domains, this effect did not differ between facts drawn from both preferred and non-preferred domains. Notably, this pattern persists in networks that are inactive for the non-preferred categories relative to baseline during unsuccessful-access or knowledge-absent trials (i.e. person and object networks, figure 4C). Thus, while it may be intuitive to expect that increases associated with semantic access to be domain-selective in domain-selective networks, the data indicates that successful access is associated with a relative broadening of the accessed semantic representations.

The place-selective network represented an exception to this pattern. In addition to showing a selective increase in response for place stimuli, these regions were also engaged during unsuccessful semantic access for both preferred and non-preferred domains. This indicates that, unlike the other knowledge-domain-selective regions, PPA, TOS and RSC are involved in searching for the knowledge. These regions show flexible cross recruitment when semantic judgements about person-related concepts (e.g. 'is a judge involved is the sale of retail goods?'), while comparable effects are not observed in person-selective regions when similar judgments are made about place-related concepts (e.g. 'is a courtroom involved is the sale of retail goods?'). Moreover, these regions are implicated in knowledge-based navigation, locating a particular street within a university campus (Epstein et al. 2007) or a particular city, the provenance of a famous person or even traditional food-dish within a country (Fairhall 2020). The present result extends the particular profile of place-selective semantic regions to show that they are also involved in the search for semantic information,

both when access is successful and when the searched-for-fact is illusive. The reason for the particular involvement of these scene- and spatially-selective regions in the search for knowledge is uncertain. An increasing body of evidence has emerged to suggest that neural mechanism for special spatial navigation in the entorhinal cortex ('grid cells') are repurposed to allow navigation across non-spatial dimensions, such as olfactory or pitch spaces (Aronov et al. 2017; Bao et al. 2019) and extending to navigation across certain conceptual spaces (Constantinescu et al. 2016; see Bottini and Doeller 2020 for a review; Viganò and Piazza 2020). One intriguing possibility is that the involvement of place-selective regions in navigation to complex factual information is derived via the interdependence between these regions and entorhinal cortices is spatial processing.

In this work, we sought to determine the processes that distinguish successful and unsuccessful semantic retrieval. By proxy, this approach allowed us to dissociate the neural processes associated with the search for a piece knowledge from access to that knowledge. We observed that prefrontal semantic control regions are involved in the search for information and are supported by cortical regions involved in scene and spatial knowledge (PPA, TOS, and RSC) for all stimulus-domains. We saw that access to knowledge recruits representational systems, and does so broadly, recruiting both regions selective for the relevant knowledge-domain and those selective for other domains. Collectively, these results suggest that prefrontal semantic control systems and classical spatial-knowledge-selective regions work together to locate relevant information and that access to a fact brings with it a broad range of associated memories incorporating other knowledge domains, rather than narrowing to information most relevant to the specific knowledge domain.

Data Availability. The full fMRI dataset along with supporting files and Matlab scripts to facilitate replication of the analyses are available at:
https://doi.org/10.5061/dryad.76hdr7swt

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References

Aglinskas A, Fairhall SL. 2020. Regional Specialization and Coordination Within the Network for Perceiving and Knowing About Others. Cereb Cortex. 30:836–848.

Aronov D, Nevers R, Tank DW. 2017. Mapping of a non-spatial dimension by the hippocampal-entorhinal circuit. Nature. 543:719–722.

Badre D, Poldrack RA, Paré-Blagoev EJ, Insler RZ, Wagner AD. 2005. Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. Neuron. 47:907–918.

Bao X, Gjorgieva E, Shanahan LK, Howard JD, Kahnt T, Gottfried JA. 2019. Grid-like Neural Representations Support Olfactory Navigation of a Two-Dimensional Odor Space. Neuron. 102:1066-1075.e5.

Bi Y, Wang X, Caramazza A. 2016. Object Domain and Modality in the Ventral Visual Pathway. Trends Cogn Sci. 20:282–290.

Binder JR, Desai RH, Graves WW, Conant LL. 2009. Where Is the Semantic System? A Critical Review and Meta-Analysis of 120 Functional Neuroimaging Studies. Cereb Cortex. 19:2767–2796.

Bottini R, Doeller CF. 2020. Knowledge Across Reference Frames: Cognitive Maps and Image Spaces. Trends Cogn Sci. 24:606–619.

Bruffaerts R, Dupont P, Peeters R, De Deyne S, Storms G, Vandenberghe R. 2013. Similarity of fMRI activity patterns in left perirhinal cortex reflects semantic similarity between words. J Neurosci. 33:18597–18607.

Buckner RL, Andrews-Hanna JR, Schacter DL. 2008. The brain's default network: Anatomy, function, and relevance to disease. Ann N Y Acad Sci.

Chao LL, Haxby J V., Martin A. 1999. Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. Nat Neurosci.

Constantinescu AO, O'Reilly JX, Behrens TEJ. 2016. Organizing conceptual knowledge in humans with a gridlike code. Science (80-). 352:1464–1468.

Devereux BJ, Clarke A, Marouchos A, Tyler LK. 2013. Representational Similarity Analysis Reveals Commonalities and Differences in the Semantic Processing of Words and Objects. J Neurosci. 33:18906–18916.

Dilks DD, Julian JB, Kubilius J, Spelke ES, Kanwisher N. 2011. Mirror-Image Sensitivity and Invariance in Object and Scene Processing Pathways. J Neurosci. 31:11305–11312.

Epstein RA, Parker WE, Feiler AM. 2007. Where Am I Now? Distinct Roles for Parahippocampal and Retrosplenial Cortices in Place Recognition. J Neurosci. 27:6141–6149.

Fairhall SL. 2020. Cross recruitment of domain-selective cortical representations enables flexible semantic knowledge. J Neurosci. JN-RM-2224-19.

Fairhall SL, Anzellotti S, Ubaldi S, Caramazza A. 2014. Person- and place-selective neural

substrates for entity-specific semantic access. Cereb Cortex. 24:1687–1696.
Fairhall SL, Caramazza A. 2013a. Brain regions that represent amodal conceptual knowledge. J Neurosci. 33.
Fairhall SL, Caramazza A. 2013b. Category-selective neural substrates for person- and place-related concepts. Cortex. 49:2748–2757.
Fernandino L, Binder JR, Desai RH, Pendl SL, Humphries CJ, Gross WL, Conant LL, Seidenberg MS. 2015. Concept representation reflects multimodal abstraction: A framework for embodied semantics. Cereb Cortex. 1–17.
Hart TJ. 1967. Memory and the feeling-of-knowing experience. J Educ Psychol. 56:208–216.
Hauk O, Johnsrude I, Pulvermüller F. 2004. Somatotopic Representation of Action Words in Human Motor and Premotor Cortex. Neuron. 41:301–307.
Jackson RL. 2021. The neural correlates of semantic control revisited. Neuroimage.
Jackson RL, Hoffman P, Pobric G, Lambon Ralph MA. 2016. The Semantic Network at Work and Rest: Differential Connectivity of Anterior Temporal Lobe Subregions. J Neurosci. 36:1490–1501.
Kikyo H, Ohki K, Miyashita Y. 2002. Neural Correlates for Feeling-of-Knowing. Neuron. 36:177–186.
Lambon-Ralph MA, Jefferies E, Patterson K, Rogers TT. 2017. The neural and computational bases of semantic cognition. Nat Rev Neurosci. 18:42–55.
Liuzzi AG, Aglinskas A, Fairhall SL. 2020. General and feature-based semantic representations in the semantic network. Sci Rep.
Liuzzi AG, Bruffaerts R, Dupont P, Adamczuk K, Peeters R, De Deyne S, Storms G, Vandenberghe R. 2015. Left perirhinal cortex codes for similarity in meaning between written words: Comparison with auditory word input. Neuropsychologia. 76:4–16.
Maril A, Simons JS, Weaver JJ, Schacter DL. 2005. Graded recall success: An event-related fMRI comparison of tip of the tongue and feeling of knowing. Neuroimage.
Maril A, Wagner AD, Schacter DL. 2001. On the tip of the tongue: An event-related fMRI study of semantic retrieval failure and cognitive conflict. Neuron.
Martin A, Chao LL. 2001. Semantic memory and the brain: Structure and processes. Curr Opin Neurobiol.
Noppeney U, Price CJ, Penny WD, Friston KJ. 2006. Two distinct neural mechanisms for category-selective responses. Cereb Cortex. 16:437–445.
Patterson K, Nestor PJ, Rogers TT. 2007. Where do you know what you know? The representation of semantic knowledge in the human brain. Nat Rev Neurosci. 8:976–987.
Peelen M V., Bracci S, Lu X, He C, Caramazza A, Bi Y. 2013. Tool selectivity in left occipitotemporal cortex develops without vision. J Cogn Neurosci.
Rabini G, Ubaldi S, Fairhall S. 2021. Combining concepts across categorical domains: a linking role of the precuneus. Neurobiol Lang.
Rubin TN, Koyejo O, Gorgolewski KJ, Jones MN, Poldrack RA, Yarkoni T. 2017. Decoding brain activity using a large-scale probabilistic functional-anatomical atlas of human cognition. PLoS Comput Biol. 13:1–24.
Schacter DL. 1999. The seven sins of memory: Insights from psychology and cognitive neuroscience. Am Psychol. 54:182–203.
Simmons WK, Reddish M, Bellgowan PSF, Martin A. 2010. The selectivity and functional connectivity of the anterior temporal lobes. Cereb Cortex.
Thompson-Schill SL, D'Esposito M, Aguirre GK, Farah MJ. 1997. Role of left inferior

prefrontal cortex in retrieval of semantic knowledge: A reevaluation. Proc Natl Acad Sci U S A.
Tyler LK, Moss HE. 2001. Towards a distributed account of conceptual knowledge. Trends Cogn Sci. 5:244–252.
Viganò S, Piazza M. 2020. Distance and direction codes underlie navigation of a novel semantic space in the human brain. J Neurosci. 40:2727–2736.
Wagner AD, Paré-Blagoev EJ, Clark J, Poldrack RA. 2001. Recovering meaning: Left prefrontal cortex guides controlled semantic retrieval. Neuron.
Whitney C, Kirk M, O'Sullivan J, Lambon Ralph MA, Jefferies E. 2011. The neural organization of semantic control: TMS evidence for a distributed network in left inferior frontal and posterior middle temporal gyrus. Cereb Cortex. 21:1066–1075.
Yarkoni T, Poldrack RA, Nichols TE, Van Essen DC, Wager TD. 2011. Large-scale automated synthesis of human functional neuroimaging data. Nat Methods. 8:665–670.