

ORIGINAL ARTICLE

Regional Specialization and Coordination Within the Network for Perceiving and Knowing About Others

Aidas Aglinskas^{1,*} and Scott L. Fairhall¹

¹Center for Mind/Brain Sciences, University of Trento, Corso Bettini 31, 38068 Rovereto, Italy

Address correspondence to: Aidas Aglinskas, Center for Mind/Brain Sciences, University of Trento, Corso Bettini 31, 38068 Rovereto, Italy.

Email: aidas.aglinskas@unitn.it.

Abstract

Seeing familiar faces prompts the recall of diverse kinds of person-related knowledge. How this information is encoded within the well-characterized face-/person-selective network remains an outstanding question. In this functional magnetic resonance imaging study, participants rated famous faces in 10 tasks covering 5 domains of person knowledge (social, episodic, semantic, physical, and nominal). Comparing different cognitive domains enabled us to 1) test the relative roles of brain regions in specific cognitive processes and 2) apply a multivariate network-level representational similarity analysis (NetRSA) to gain insight into underlying system-level organization. Comparing across cognitive domains revealed the importance of multiple domains in most regions, the importance of social over nominal knowledge in the anterior temporal lobe, and the functional subdivision of the temporoparietal junction into perceptual superior temporal sulcus and knowledge-related angular gyrus. NetRSA revealed a strong divide between regions implicated in “default-mode” cognition and the fronto-lateral elements that coordinated more with “core” perceptual components (fusiform/occipital face areas and posterior superior temporal sulcus). NetRSA also revealed a taxonomy of cognitive processes, with semantic retrieval being more similar to episodic than nominal knowledge. Collectively, these results illustrate the importance of coordinated activity of the person knowledge network in the instantiation of the diverse cognitive capacities of this system.

Key words: cortical network, face perception, fMRI, representational similarity analysis, semantics

Introduction

Seeing a familiar person brings to awareness a variety of related attributes: biographical facts (semantic knowledge), personal experiences (episodic knowledge), perceptual attributes (physical knowledge), trustworthiness (social knowledge), and their name (nominal knowledge). We use this wealth of person-specific information frequently in our day-to-day lives. The question of how this diverse information is represented in the brain is an area of active research.

Neuroimaging studies have identified an interconnected network of regions activated when we see and think about other people (Haxby et al. 2000; Gobbini and Haxby 2007; Fairhall and Ishai 2007). This network is composed of a perceptual “core system”, the occipital face area (OFA) and

fusiform face area (FFA) (Kanwisher et al. 1997; Gauthier et al. 2000), and the posterior superior temporal sulcus (pSTS). This core is complemented by an “extended system”—a more loosely grouped set of regions implicated in a broad range of person-related cognition less related to perception (Haxby et al. 2000). The extended system includes lateral frontal regions: inferior frontal gyri (IFG) and lateral orbitofrontal cortex (OFC); as well as the anterior temporal lobes (ATLs), precuneus, ventromedial prefrontal cortex (vmPFC), and dorsomedial prefrontal cortex (dmPFC); and medial temporal regions: the amygdalae and potentially—the recently identified, face-selective anterior temporal face patch (ATFP) Moeller et al. 2008; Rajimehr et al. 2009; Von Der Heide et al. 2013).

Numerous investigations of the contribution of these regions have produced diverse, and at times discordant, results (Table 1).

Table 1 Illustrates complex cognitive landscape of the attribution of cognitive roles to various regions of the person knowledge network

Brain region	Cognitive function
OFA	Perception (Adolphs 2002, 2003; Gobbini and Haxby 2007; Wieser and Brosch 2012)
FFA	Perception (Adolphs 2002, 2003; Gobbini and Haxby 2007; Minnebusch and Daum 2009; Wieser and Brosch 2012; Werner et al. 2013)
OFC	Motivation and reward (Bortolon et al. 2015) Top-down modulation of OFA, FFA (Bortolon et al. 2015) Emotion (Adolphs 2002)
IFG	Semantic knowledge (Gobbini and Haxby 2007) Working memory (Adolphs 2003) Perception (Adolphs 2003; Calder and Young 2005; Minnebusch and Daum 2009) Naming (Adolphs 2002) Attractiveness and physical knowledge (Bzdok et al. 2010)
Precuneus	Familiarity (Adolphs 2003; Werner et al. 2013) Episodic knowledge (Adolphs 2003; Gobbini and Haxby 2007; Patterson et al. 2007; Wieser and Brosch 2012) Personality traits (Murray, et al., 2012)
vmPFC	Social knowledge and personality traits (Adolphs 2003; Adolphs 2002; Werner et al. 2013) Mental states (Gobbini and Haxby 2007; Wieser and Brosch 2012) Emotion (Werner et al. 2013) Attractiveness and physical knowledge (Bzdok et al. 2010)
ATL	Semantic knowledge (Adolphs 2003; Gobbini and Haxby 2007; Olson et al. 2007; Wieser and Brosch 2012) Identity representation (Adolphs 2003) Naming (Calder and Young 2005; Olson et al. 2007; Patterson et al. 2007) Familiarity (Olson et al. 2007; Werner et al. 2013) Social knowledge (Olson et al. 2013)
pSTS	Perception (Adolphs 2003) Social knowledge and mental states (Gobbini and Haxby 2007; Wieser and Brosch 2012)
Amygdala	Emotion (Gobbini and Haxby 2007) Physical knowledge (Bzdok et al. 2010) Social knowledge (Bzdok et al. 2010)
ATFP	Familiarity (Ross and Olson 2011; Von Der Heide et al. 2013) Identity representation (Ross and Olson 2012)

We sampled published reviews and meta-analyses reporting regional function in the context of person perception/knowledge. Attributions have been broadly grouped into the categories such as perception, semantic knowledge, or working memory.

For example, while the pSTS is classically characterized as a core “perceptual” region, it is frequently linked with social and other person-related cognition that is unrelated to perception (Adolphs, 2003; Fairhall and Caramazza 2013a; Koster-Hale et al. 2017), potentially linked to the marked heterogeneity of the broader temporoparietal junction (TPJ) (Gobbini and Haxby 2007; Hein and Knight 2008). Likewise, the varied functional attributions of the ATL to proper naming (Grabowski et al. 2001), semantic information (Tippett et al. 2000; Glosser et al. 2003; Olson et al. 2007), and social cognition (Frith, 2007) illustrate further the diversity and complexity of regional roles within the extended system (see Simmons and Martin 2009 for discussion).

Much insight has been gained from research addressing single cognitive function in one or a few brain areas. However, this approach has the potential to ambiguate the true functions of regions. Uncertainties surrounding regional function are expounded by the tendency of research to address single cognitive functions in one or a few brain areas. Most regions of the extended system are recruited to some extent across multiple experimental contexts, including simple tasks such as repetition detection (Todorov et al. 2007) or superordinate categorization (Fairhall et al. 2014). In other words, most all person-related cognition involves most all of the extended system. The important information may not be whether a specific region is modulated by a task but the “relative” change of regional

activity across the entire network. Rather than attributing a function to a region or a region to a function, it may be that the representation of cognition within the brain is best described in terms of the patterns of activation over distributed cortical networks.

The importance of network over region is especially important considering that many elements of the extended system fall within one prominent network in the brain, the intrinsic brain network—a collection of brain regions associated with a range of internalized cognitive processes (Spreng et al. 2010). Internalized cognition refers not only to “default-mode”, task-deactivated states (Raichle et al. 2001) but also a broad range of internalized cognitive processes: general semantic knowledge (Binder et al. 2009; Fairhall and Caramazza 2013b; Huth et al. 2016) and social cognition (Greene et al. 2001; Van Overwalle 2009, 2011), as well as context integration episodic memory and mental time travel (Schacter and Addis 2007; Keidel et al. 2017; Viard et al. 2011). As elements of the internalized cognition network are frequently activated together, establishing specific contributions of each region has proved challenging (Moran et al. 2011; Van Overwalle 2011).

In this work, we isolate the network activated when we view familiar faces during a simple stimulus repetition detection task. We then push the network toward different aspects of person knowledge (social, semantic, episodic, nominal, and physical) to understand the relative importance of these processes to each

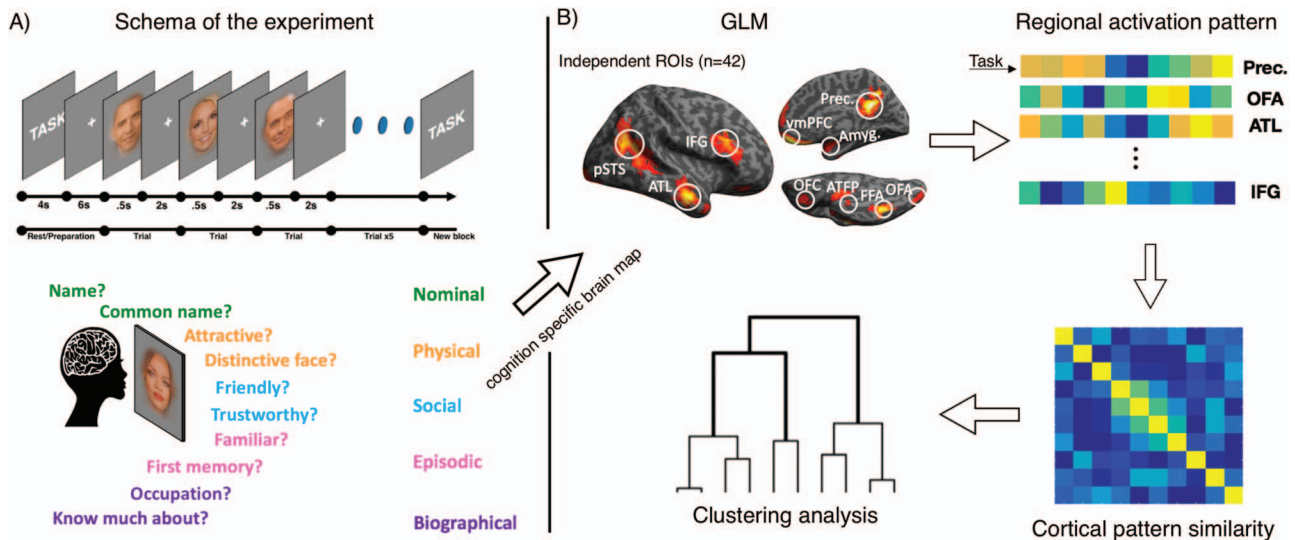


Figure 1. (A) Top: schematic representation of the experiment. Experimental blocks were preceded by 4 s of instruction screen and 6 s fixation point. Each trial consisted of 0.5 s face presentation and 2 s fixation. Bottom: 5 domains of person knowledge and 2 questions per domain are noted in corresponding colors. (B) Data analysis schematic. ROI beta averages for each of the 10 tasks were extracted from ROIs, correlated, and subjected to representational similarity analysis (RSA).

region. The goals of the current experiment are 3-fold. The first is to re-examine the roles of key brain regions in cognitive function by considering these regions both in context of different cognitions and other brain regions. Specifically, we investigate the role of the ATL in social cognition and nominal knowledge and the role of the pSTS and AG in access to person knowledge. Our second goal is to apply network-level representational similarity analysis (NetRSA). NetRSA entails a multivariate approach based on the regional response magnitude within network nodes, with the multivariate element coming from the changing regional biases across different tasks. We employ NetRSA to address 2 questions: 1) how are cognitive domains represented across the network and 2) how do these regions work together to accomplish the diverse range of ensemble functions of the network. We hypothesize that all person knowledge regions are involved across all cognitive dimensions related to other people and that the cognitive flexibility of this system lies within subtle differences in the pattern of activation across the network. Lastly, it is important to consider that these core and extended systems presumably pair and couple with brain regions outside the person-selective network, with the network's periphery potentially influencing activity within this network. Diverse kinds of person knowledge most likely depend on the interaction of both common and distinct neural mechanisms.

Materials and Methods

Participants

A total of 20 right-handed, native Italian participants (8 males: mean age, 23.2 years; range, 19–32 years) took part in this study. The specific number of subjects ($N=20$) was decided based on previous research investigating person knowledge access effects (such as occupation or nationality; e.g., Fairhall and Caramazza 2013a; Fairhall et al. 2014). Participants had normal or corrected-to-normal vision and no history of neurological incidents. The study was approved by the University of Trento ethical committee. All participants gave informed consent and were compensated for their time.

Stimuli

Stimuli were 40 pictures of famous faces and 40 pictures of famous buildings. The stimulus set consisted of Italian and foreign politicians, actors, singers, and sportsmen, as well as landmarks (Eiffel Tower, Colosseum). Stimuli were cropped with a face-shaped mask, and the eyes and mouth were aligned across faces. Stimuli extended 400 pixels vertically and 300 pixels horizontally and were presented centered on the screen (1280×1024 resolution, 60 hz refresh rate), with gray background. After the experiment, 13/20 participants were presented with faces they saw in the experiment and asked whether they recognized the celebrity. On average, the subjects recognized $M=84\%$ of faces, 95% confidence interval = 76.4%–91.6% suggesting a reasonable recognition rate, which is consistent with behavioral performance experimental tasks performed in the scanner (see below: behavioral results).

Task

Each experimental block started with 4 s instruction screen specifying the task, followed by 6 s of fixation cross. After that, a face was presented for 0.5 s followed by 2 s of fixation cross during which subjects provided a response via button box. Within each 8-trial block, participants were instructed to respond to questions covering 5 categories of person knowledge: episodic memories, semantic knowledge, social judgments, nominal knowledge, and physical knowledge. For each of the categories, we chose 2 different probe questions that require access to each kind of knowledge (totaling 10 experimental tasks; see Fig. 1 and Table 2). In addition, there were 2 1-back matching control tasks with either pictures of faces or famous monuments. The experiment consisted of 5 runs (8 min, 42 s each). A total of 16 blocks were presented in a randomized order (1 block for each task plus 3 face and 3 monument 1-back control blocks).

Participants answered 9/10 questions using a 1–4 Likert scale. Occupation question (“what is this persons’ occupation”) had predefined categories (1 = actor or TV presenter, 2 = singer

Table 2 Experimental questions

Knowledge category	Task cue	Participant instructions	Answer choices
Nominal	Common name	How common is this person's name?	Likert scale (1–4)
	Full name	How well can you recall the person's full name?	Likert scale (1–4)
Physical	Attractive	How attractive do you find this person?	Likert scale (1–4)
	Distinctive	How distinctive is this person's face?	Likert scale (1–4)
Social	Friendly	How friendly is this person?	Likert scale (1–4)
	Trustworthy	How trustworthy is this person?	Likert scale (1–4)
Episodic	Familiar	How familiar is this person to you?	Likert scale (1–4)
	First memory	For how long have you known this person?	Likert scale (1–4)
Semantic	How many facts	How many facts could you recall about this person?	Likert scale (1–4)
	Occupation (see 'task')	What is this person occupation?	Predefined categories

We selected 5 categories of person-related knowledge (nominal, physical, episodic, social, and semantic). For each category, we chose 2 different probe questions that require accessing the specific category of knowledge. Each task was presented in a block of 8 trials. On each trial, participants were instructed to relate the task question to the famous person.

Table 3 ROI sphere center coordinates

Region	Hemisphere	X	Y	Z	ROI size
Precuneus	Medial	3	–52	29	81
	Right	30	–91	–10	65
OFA	Left	–33	–88	–10	49
	Right	42	–46	–22	81
FFA	Left	–39	–46	–22	30
	Right	39	17	23	44
IFG	Left	–36	20	26	38
	Left	–60	–7	–19	69
ATL	Right	57	–7	–19	81
	Left	–21	–10	–13	62
Amygdala	Right	21	–7	–16	59
	Medial	6	59	23	59
dmPFC	Medial	3	50	–19	66
vmPFC	Right	33	35	–13	58
	Left	–33	35	–13	27
OFC	Right	33	–10	–40	39
	Left	–36	–10	–34	24
ATFP	Left	–48	–67	35	68
	Right	42	–64	35	57
Angular	Left	–48	–49	14	54
	Right	48	–55	14	71

Peak coordinates for regions active in the localizer experiment ($N = 42$) and ROI sizes in voxels after thresholding. Coordinates are in MNI space.

or musician, 3 = politician or sportsman, and 4 = none of the above). Prior to scanning, participants practiced answering experimental questions on a different set of famous people repeating each question for 5 trials.

Data Acquisition

Participants were scanned at the Center for Mind/Brain Sciences (CIMEC), University of Trento, Italy. Data were collected using Bruker BioSpin MedSpec 4T, with 8-channel phased-array head coil. A total of 5 runs of 209 echo-planar volumes, consisting of 34, AC-PC aligned axial slices were acquired while participants performed the task (field of view (FOV) = 64 mm × 64 mm, time repetition = 2.5 s, time echo = 33 ms, flip angle = 73°). Voxel size was 3 × 3 × 3 mm with a 1 mm gap. In addition to no change, a whole-brain T1-MPRAGE anatomical image was acquired [whole brain (FOV = 256 × 224, 176 1 mm axial slices)].

ROI definition

Regions of interest (ROIs) were selected from an independent ($N = 42$) experiment, conducted for high-power functional localization. In the localizer experiment, participants performed a 1-back matching task with 12-s blocks of famous faces, common animals, or common objects. The contrast faces > animals + tools ($P < 0.05$ family-wise error (FWE) corrected) was used to identify face-selective peaks (Table 3). A total of 21, 7.5mm radius spheres were drawn around the peak voxels, and task-evoked brain responses (beta estimates) were extracted for each subject.

To investigate differences in pSTS/angular gyrus (see Introduction), we anatomically constrained the volume with angular and superior temporal gyri masks. Then the masks were inflated, and the overlap was removed. This allowed us to distinguish face-selective anatomical activation within anatomical angular and superior temporal gyri within anatomical boundaries.

Data Analysis

Data were preprocessed with SPM12. Functional images were realigned to account for motion, gray matter segmented, warped into common space, and smoothed with 8-mm full-width half-maximum kernel. Subject-specific response estimates (beta weights) were derived by fitting a general linear model to the data. A total of 12 regressors (10 tasks and 2 controls) were included as explanatory variables. A total of 6 motion parameters from realignment procedure were included as regressors of no interest.

To mediate anatomical specificity and signal strength, we drew 7.5-mm radius spheres around the chosen coordinates [diameter = 5 voxels (voxel size, 3mm³); we then extracted the mean beta value from voxels within those ROIs that were significantly active at $P < 0.001$ (contrast faces > animals + tools, see Table 3 for location and extent). To baseline the cognitive response with respect to perceptual effects elicited by viewing faces, within each region, the activation from the control condition was subtracted from task activation. Activity during the experimental (person knowledge) tasks did not factor in the localization procedure.

Multivariate Analyses

ROI responses across tasks were averaged across voxels and correlated to obtain a dissimilarity matrix (1-r), which was then subjected to Ward hierarchical agglomerative clustering. For task similarity analysis, the matrix was transposed before correlating so that similarity matrix consisted of task correlation across ROIs.

Results

Behavioral Data

Mean reaction time (RT) was $M = 1203$ ms, standard deviation (SD) = 111 ms. Subjects reacted fastest during full name task ($M = 1110$ ms, SD = 120 ms) and slowest during common name task ($M = 1386$ ms, SD = 200 ms). RTs differed across the 10 tasks [$F(9, 171) = 17.13$, $P < 0.001$]. Critically, this RT effect did not persist when tasks were collapsed into the 5 domains of knowledge used in the imaging analysis [i.e., “nominal”, “physical”, “social”, “episodic”, and “semantic”; $F(4, 95) = 2.21$, $P = 0.076$]. RT did not significantly differ between face ($M = 0.71$, SD = 0.11) and place ($M = 0.68$, SD = 0.12) control 1-back matching tasks ($t(18) = 1.96$, $P = 0.066$). Participants correctly indicated the occupation of $M = 84\%$ (standard error of the mean (SE) = 3.2%) famous people, consistent with the explicit recognition responses of the 13/20 participants who completed the postscanning recognition task. Likewise, participants could recall between “few” to “a lot” of biographical facts for $M = 82\%$ (SE = 2.7%) of the stimulus faces. The average confidence rating for knowing the target individuals full name was 1.82, between “1” very highly confident and “2” highly confident. Across all tasks, faces were rated lowest on attractiveness ($M = 2.79$, SD = 0.025) and highest on participants’ ability to recall full name ($M = 1.82$, SD = 0.38) (lower numbers indicate higher agreement with task statement). Ratings differed across 10 exemplar tasks [$F(4.8, 91.7) = 27.741$, $P < 0.001$, Greenhouse–Geisser correction] and 5 cognitive domains [$F(4, 76) = 20.03$, $P < 0.001$]. To check whether task ratings influence task representation in the brain, we constructed a representational similarity model of similarly rated tasks and compared it to task similarity across the network

(see cognitive taxonomy). The relationship between rating similarity and cognitive taxonomy did not approach significance [$t(19) = 0.78$, $P = 0.442$].

fMRI Results

Accessing Person-Related Knowledge Recruits Extended, Not Core, Components

To assess the global importance of access to person knowledge in the core and extended systems for person perception/knowledge, we compared the average regional increase when participants accessed the 10 variants of person knowledge, compared to the 1-back matching task on famous faces. The results are shown in Figure 2.

The most apparent distinction is between regions of the core system, which show no increase in activity [$t(19) = -1.69$, $P = 0.11$; averaged across all core regions] and other elements of the network [$t(19) = 6.98$, $P < 0.001$; averaged across all extended regions].

A second clear organizational feature of person knowledge is the left lateralization of this process, with left hemisphere regions showing a greater relative increase when accessing person knowledge than their right hemisphere counterparts [$t(19) = 4.67$, $P < 0.001$].

Individually, regions of the internalized cognition part of extended system were all strongly recruited during access to person knowledge ($t > 4.60$, $P < 0.001$). Lateral frontal regions, the IFG, and lateral OFC show an increased response most consistently in the left, with the right IFG failing to show a significant modulation. More subtle increases are seen in medial temporal lobe structures, with only the left amygdala and the right ATL exhibiting significant modulation when person knowledge was accessed.

The Role of Cognitive Domain Across the Person Knowledge Network

To investigate the role of different kinds of knowledge in the person knowledge network, Figure 3 shows the scaled importance of each cognitive domain in those regions that were activated during access to person knowledge. Specifically, the height of each stacked bar indicates the percentage of the total signal elicited across all domains. Here we focus only on regions that showed at least a significant unilateral increase when person knowledge is accessed. For simplicity, we have collapsed across hemisphere [significant interaction between domain and hemisphere were present only in IFG; $F(4, 76) = 2.508$, $P = 0.049$]. Regions of the intrinsic network are strongly involved in all cognitive domains with the exception of nominal knowledge, to which ATL and dmPFC were unresponsive.

The ATL Is Weighted Toward Social Not Nominal knowledge

The involvement of ATL in social or nominal (proper names) knowledge is a matter of current contention (Grabowski et al. 2001; Olson et al. 2013). We exploited the presence of all these cognitive aspects within one single study to address their relative importance in bilateral ATL. Analysis of variance (ANOVA) revealed significant differences across cognitive domains [$F(4, 95) = 8.13$, $P < 0.001$]. A planned comparison specifically testing the role of social and nominal tasks revealed that access to

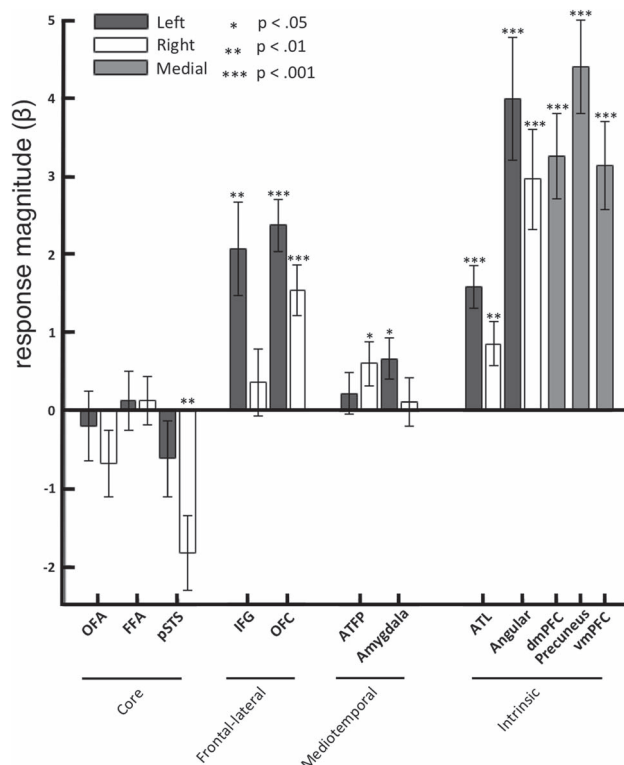


Figure 2. Regional response to person knowledge access (average of experimental tasks > face control task). Bars show response estimate magnitude (beta value); error bars represent standard error of the mean (SE). Retrieving person knowledge activated extended system regions to variable extent, but core system did not show an increased response.

social knowledge recruited this region to a greater extent than access to nominal knowledge [$t(19) = 5.79$, $P < 0.001$], with nominal knowledge showing marginal increase compared to control [$t(19) = 2.08$, $P = 0.052$]. This effect persists even when considering only famous people whose names participants could recall with high to very high confidence [social > nominal $t(19) = 6.32$, $P < 0.001$]. Follow up analyses revealed that while the largest response was evident during access to social knowledge, this was not significantly greater than episodic, semantic, or physical cognitive domains, each of which showed a greater response than the nominal tasks (post hoc: all $t > 2.49$, all $P < 0.02$, uncorrected). The response during the nominal tasks was not diminished in all regions, with IFG responding more strongly to access to nominal than social knowledge [$t(19) = 3.1$, $P = 0.006$]. These results show a distinction between the way social and nominal knowledge is processed, social tasks engage ATL more than nominal ones, while the IFG exhibits the opposite pattern, being more responsive to nominal than social knowledge.

Perceptual and Nonperceptual Processing in the pSTS/Angular Gyrus

Here we sought to test whether the pSTS and AG have diverse functional roles. While these regions sometimes form a contiguous activation cluster, pSTS has been implicated in perceptual processes, while AG is involved in cognitive processes such as intent and mental state processing (Gobbini and Haxby 2007). The functional division between these 2 regions was apparent even at a level of global access to person knowledge (c.f. Fig. 2).

Specifically, while the pSTS showed a suppressed response during access to stored person knowledge [pSTS left: $t(19) = -1.26$, ns.; right: $t(19) = -3.81$, $P = 0.001$], the angular gyrus conversely showed a robust response [AG left: $t(19) = 5.81$, $P < 0.001$; right: $t(19) = 2.99$, $P = 0.008$]. This difference was also apparent in the global laterality pattern. pSTS showed a stronger inhibition in response on the right [$t(19) = 3.47$, $P = 0.001$], consistent with the pattern of right laterality in core regions. Conversely, there was no laterality effect in global response of the angular gyrus [$t(19) = 1.57$, $P = 0.134$]. Collectively, these patterns underscore the pronounced functional subdivision of these regions of the TPJ.

At the level of a single cognitive domain (see Fig. 3), an increased response in AG was evident across each cognitive domain ($t > 3.12$, $P < 0.006$) while the pSTS did not show an increase for any cognitive domain. Finally, while cognitive domain did not have a variable effect in pSTS at the univariate level, the angular gyrus responded more during episodic memory retrieval than any other task ($t > 2.8$, $P < 0.01$). Together, these results demonstrate a pattern of response in the pSTS consistent with core perceptual processing and a pattern in the AG consistent with general access to person knowledge, including each of the domains investigated in the present study. Differences in interregional coordination patterns will be discussed in the next section.

Interregional Coordination and Network Organization

A primary motivation for this study was to understand how brain regions work together during access to the varied and diverse types of person knowledge. The functional coordination between ROIs was examined through a “NetRSA”. The 10 task-induced beta patterns were correlated between each pair of ROIs and subjected to hierarchical clustering analysis (see Fig. 1 and methods). The validity of this NetRSA approach is confirmed by the close proximity of left and right regional homologs (Fig. 4). In all cases, despite the anatomical distance, a given ROI’s cognitive profile matched most closely to that of its contralateral counterpart. An RSA template model (Fig. 4), confirmed the high reliability of this effect across subjects [$t(19) = 13.89$, $P < 0.001$]. This result highlights the commonality of function between hemispheric homologs despite hemispheric asymmetries in the overall response.

At a descriptive level, NetRSA revealed the expected cognitive clustering of core regions (OFA, FFA, and pSTS). Interestingly, the lateral frontal regions, the orbitofrontal, and IFG cluster with the core system, rather than the other components of the extended system (Fig. 4—red cluster). To test whether lateral frontal regions coordinate more closely with core or extended systems, we built competing models of regional coordination (see Fig. 4). Post hoc comparisons of the goodness of fit between the 2 competing models confirmed that lateral frontal regions coordinate more closely with core than other extended system regions [$t(19) = 3.09$, $P = 0.006$]. Considering regions separately, this effect persisted for IFG [$t(19) = 4.35$, $P < 0.001$], while no preference was evident for OFC [$t(19) = 1.59$, $P = 0.13$].

Within the extended system, regions overlapping with those associated with internalized cognition form a distinct cluster (Cluster 2—green) with respect to the amygdala and anterior face patch of the medial temporal lobe (Cluster 3—purple). However, planned comparison of whether the ATP groups more closely with the core or extended system resulted in no evidence for either hypothesis [$t(19) = -0.21$, $P = 0.84$].

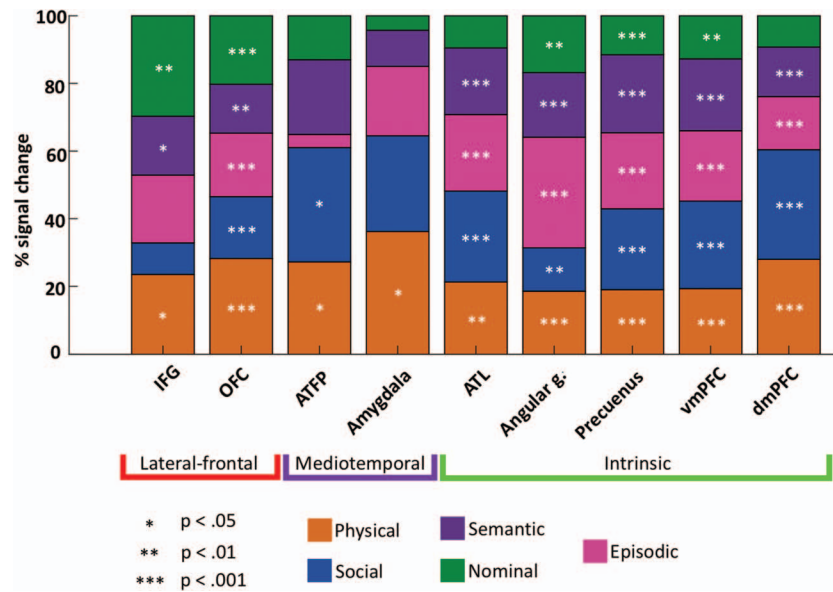
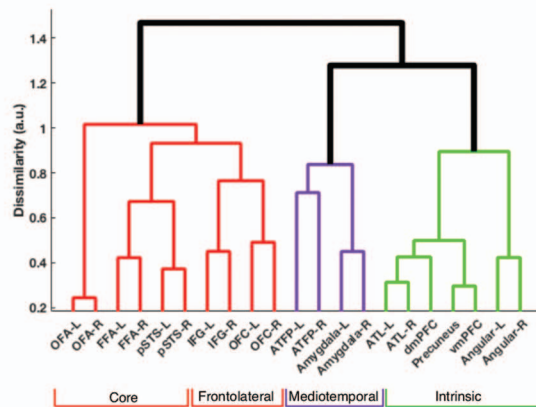


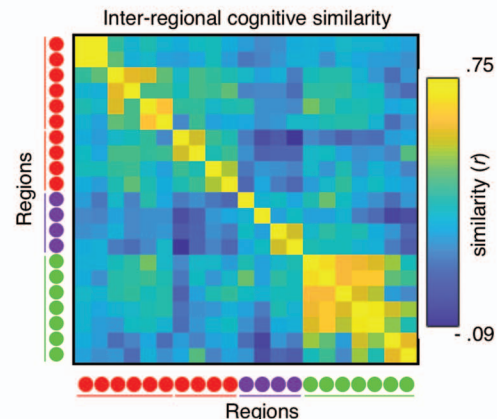
Figure 3. Regional preference patterns. Percentage of total activation elicited by each cognitive domain. Stars denote significance (uncorrected) of regional involvement in a specific person knowledge domain compared to the face-matching baseline condition. Most regions are involved in most cognitive domains, and no brain regions appear to be driven by a single cognitive domain. However, subtle patterns can be seen in the variations of loadings of particular domains in different brain regions. Regions have been grouped into lateral frontal, mediotemporal, and intrinsic subnetworks.

Network organisation: regional pattern similarity

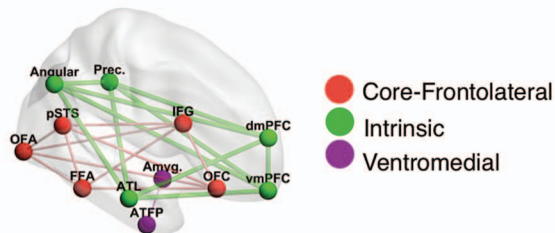
A) Hierarchical clustering



C) Model comparison



B) Anatomical schematic of network connections



Network organisation models

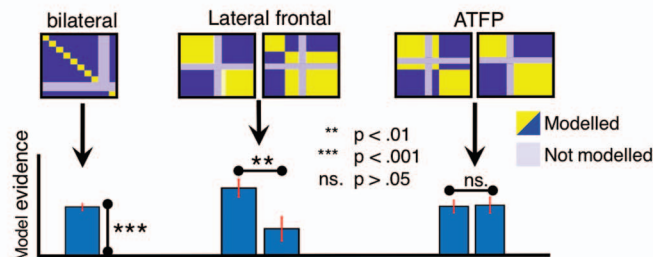


Figure 4. (A) ROI clustering. First major division separates core together with IFG and OFC from the rest of the extended system (red vs. [green + purple]). Within the extended system, a further division is evident between medial temporal regions and regions involved in the intrinsic system (purple and green). (B) Schematic representation of clusters projected onto the brain. (C) Model comparison schematic. Competing models of network organization were constructed, fitted to observed data for each participant, and compared in a paired samples t-test.

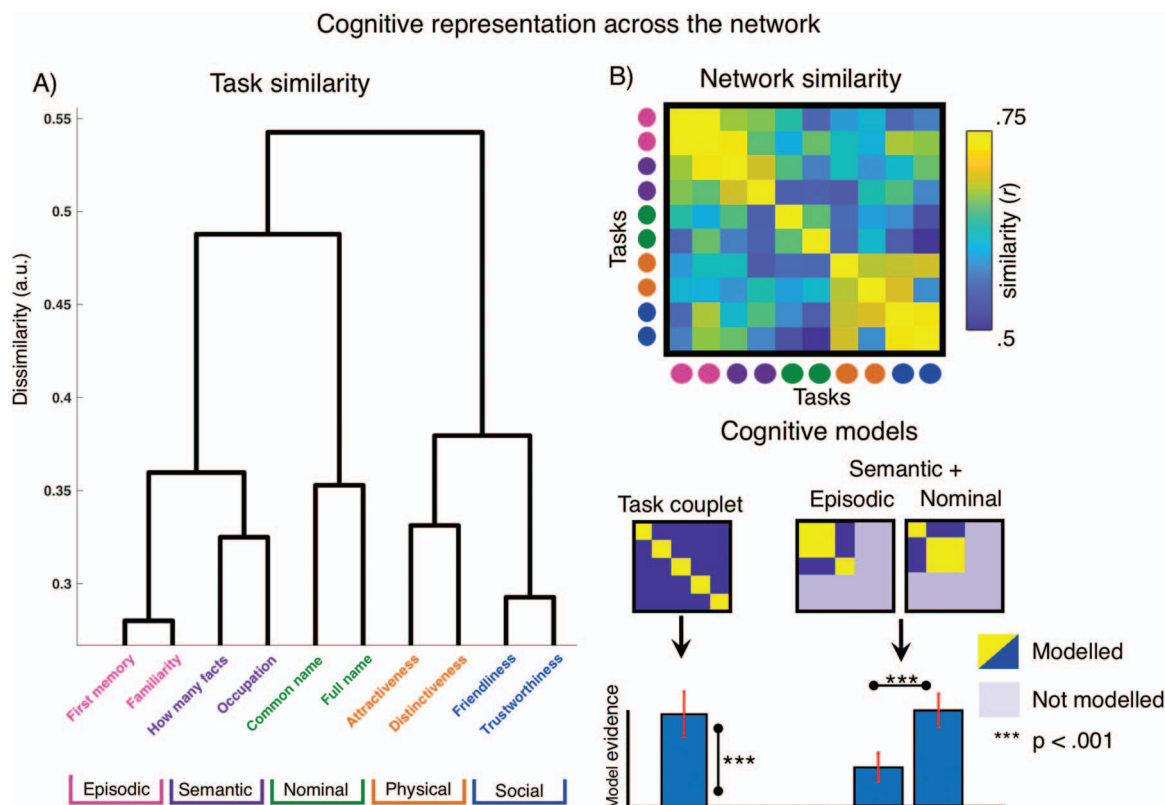


Figure 5. (A) Task similarity in core and extended system ROIs. Tasks are grouped according to the domain they were sampled from. Episodic and semantic knowledge retrieval tasks elicit differentiable patterns from nominal, physical, or social ones (dendrogram, left). (B) fMRI pattern similarity matrix and models tested.

Cortical Similarity between Cognitive Domains

To address the fundamental question of how different forms of cognition relate to one another, NetRSA was performed across ROIs to investigate how similar the neural representations of cognitive domains are in the brain (see Fig. 5 and methods). Despite variance across tasks, RTs, and in one case—response scales, the task pairs for each cognitive domain (e.g., “common name” and “full name” for nominal knowledge) are grouped together. This illustrates the efficacy of NetRSA in this context, providing another internal validation. To test our a priori selection of task couplets, we built a model to test their similarity. Results show that tasks from the same cognitive domain have highly similar representation across the person knowledge network [$t(19) = 4.14$, $P < 0.001$].

At the next level of hierarchical clustering, results reveal 3 distinct cognitive clusters. Network activity is more similar for physical (yellow) and social (blue) knowledge than to other forms of knowledge. Likewise, episodic (pink) and semantic (purple) knowledge form a cluster, which is distinct from nominal knowledge (green). We compared competing models (see Fig. 5) to make inference about whether semantic knowledge more closely relates to the episodic or nominal domain. Results confirm that semantic knowledge is more similar to episodic memories than nominal knowledge [$t(19) = 3.97$, $P < 0.001$].

Whole-Brain Analysis—Beyond the Person-Selective Network

While previous analysis focused on the network for perceiving and knowing about others, it is important to consider brain

regions outside the person-selective network that may drive transient specialization within the network itself. A whole-brain analysis comparing each cognitive domain to the average of the other domains is presented in Figure 6. Notably, no regions demonstrated a significant preference for 2 or more cognitive domains, consistent with nonoverlapping cognitive specialization outside the person knowledge network. Access to nominal knowledge is characterized by a broad pattern of activation, stronger in the left hemisphere than the right (Fig. 6 and Table 4). It encompasses left hemispheric sites associated with language production and comprehension (Price, 2012). Conversely, accessing physical knowledge is more pronounced in the right hemisphere, predominantly in the superior portion of the IFG. Social knowledge retrieval more strongly activated left ATL and an anterior patch of dmPFC. Recalling episodic memories involved the posterior cingulate cortex (PCC), angular gyrus as well as right lateral frontal pole and bilateral patches of the superior frontal gyrus. We found no involvement of the hippocampus in episodic knowledge tasks. Even at uncorrected thresholds, no significant voxels were evident. Semantic knowledge retrieval tasks did not selectively recruit any region outside of the person knowledge network.

Discussion

Cognitive processes are distributed across networks of regions. By having our participants perform a broad range of cognitive tasks and exploiting data complexity through derivations of statistical tools such as RSA, we could focus on the subtle differences in interregional coordination that endow distributed corti-

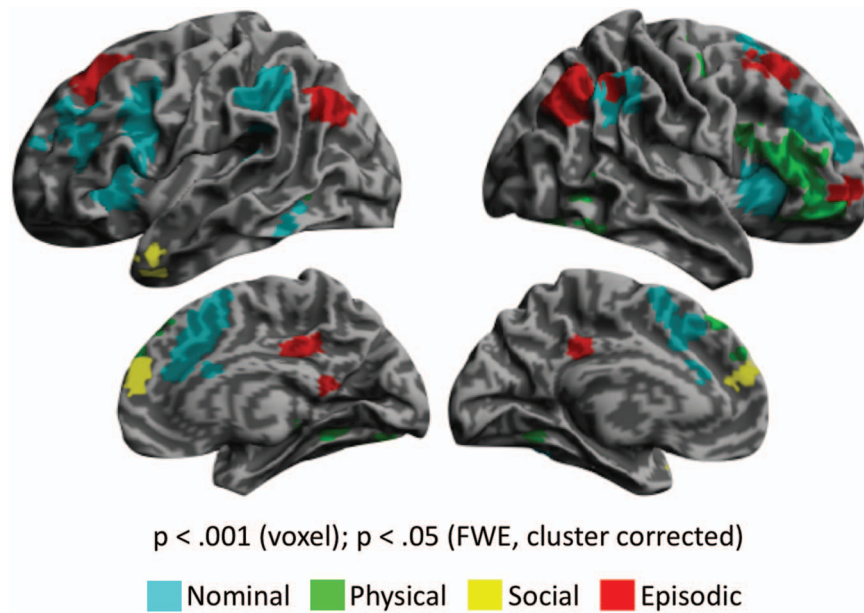


Figure 6. Cognition selective brain activations. Whole-brain map depicting domain selective cognitive systems outside the person knowledge network. Maps represent the contrast of each cognitive domain against the 4 other domains. Semantic knowledge did not elicit significant clusters of activity.

Table 4 Peak location, extent, and cluster-level significance of whole-brain analysis of the differential effects of each cognitive domain (see also Fig. 6)

Domain	Region	Hemisphere	Cluster		Peak
			P (FWE)	Size	T
Episodic	Angular	Right	< 0.001	507	8.06
	Angular	Left	< 0.001	264	6.57
	SFG	Right	< 0.001	216	5.68
	PCC	Medial	< 0.001	142	5.68
	SFG	Left	0.001	125	4.77
	OFC	Right	0.017	71	4.65
	Precuneus	Medial	0.032	61	4.16
Social	dmPFC	Medial	< 0.001	396	6.57
	ATL	Left	0.001	130	4.58
	IFG	Right	< 0.001	616	5.72
	FFA	Right	< 0.001	274	4.86
Physical	PMC	Right	0.006	87	4.38
	Amygdala	Right	0.020	68	4.37
	dmPFC	Medial	< 0.001	253	4.34
	FFA	Left	0.004	94	4.24
	IPS	Right	0.005	92	3.93
	IFG	Left	< 0.001	1188	6.99
	SFG	Medial	< 0.001	1670	6.40
Nominal	Angular	Left	< 0.001	370	6.35
	Angular	Right	< 0.001	265	5.31
	FFA	Left	0.003	97	4.70

SFG means superior frontal gyrus; IPL, inferior parietal lobule; PMC, premotor cortex.

cal networks their considerable cognitive flexibility. By relating task activity not only to a baseline but also to other tasks, we were able to establish regional preferences, which allowed us to tackle specific hypotheses about regional function. Leveraging multivariate methods provided insight into regional coordination, uncovering principles of network organization, as well as the similarity between different cognitive processes allowing us to build a cognitive taxonomy grounded in brain representation.

Accessing Person-Related Knowledge Recruits Extended, Not Core, Components

Clear functional division between core and extended system can be seen even at the broadest view of systems organization. Face-selective core regions (OFA, FFA, and pSTS) were not responsive to person knowledge tasks. This stands in contrast of the extended system regions, which were strongly engaged by the experimental tasks and particularly so in the left hemisphere.

This is consistent with a predominant role of these regions in the extraction of perceptual information, which is made available to the other elements of the system (c.f. [Downing and Peelen 2011](#)).

Functional Subdivisions Between pSTS and Angular Gyrus

The pSTS was originally designated as part of the core system (Haxby et al. 2000b). Over the years, this classification has become less clear and pSTS has been reclassified as part of both core and extended systems ([Gobbini and Haxby 2007](#)). The pSTS is part of a heterogeneous cortical region, the temporal parietal junction (TPJ), which includes pSTS, the angular gyrus, and the supramarginal gyrus. In this study, we anatomically divided the person-selective patch into pSTS and angular gyrus components. We observed a pronounced dissociation across this subdivision. Firstly, compared to the face repetition detection control task, AG exhibited a strong global response to access to person-related knowledge while pSTS was either unresponsive (left) or suppressed (right). Secondly, the response profile across cognitive tasks grouped them differently, with pSTS clustering with other core regions while AG clustered with regions of the extended system associated with intrinsic cognition.

These results indicate that the contiguous TPJ activation reported during the viewing of familiar faces is functionally heterogeneous, divided into an angular gyrus component that responds to nonvisual theory of mind ([Saxe and Powell 2006](#)) and amodal access to person knowledge ([Fairhall and Caramazza 2013a](#)) and a pSTS component involved in face perception. Future work will determine how these anatomically adjacent brain regions coordinate across other cognitive processes but within the context of person-related cognition, they appear to be highly distinct.

Regional Tuning of ATL

Different hypotheses propose that ATL might mediate person-specific social knowledge ([Olson et al. 2007](#)) or proper naming ([Semenza 2011](#)). Here we directly contrasted these 2 hypotheses and observed that ATL responds strongly to social knowledge and is unresponsive to nominal knowledge retrieval. This is in apparent contrast to early positron emission studies, which show strong activation of the region during overt naming ([Gorno-Tempini et al. 1998](#); [Grabowski et al. 2001](#)). However, it is consistent with the finding that the ATL responds equally to familiar people whether or not the name is known by the participant ([Gesierich et al. 2011](#)). The reason for these disparities may lie in functional magnetic resonance imaging (fMRI) signal drop-off in the ATL ([Devlin et al. 2000](#)) or in specific representational or phonological demands associated with overt speech production. Alternatively, it may be that ATL activation observed in earlier studies was not specific to nominal knowledge but rather to generalized activation of person knowledge. Indeed, this generality is evident in the present study where access to semantic, episodic, and physical cognitive domains, as well as social, activated ATL. It is noteworthy that while social knowledge did not produce a stronger response in the ATL ROI than these other 3 domains, the whole-brain analysis ([Fig. 6](#)) only social knowledge showed a significant cognitive selective response in adjacent the left ATL, consistent with the importance of social conceptual knowledge in this region ([Simmons and Martin 2009](#)).

Regional Coordination Across the Person Knowledge Network

Elements of the network for person knowledge coordinate to form its diverse range of functions. Here, in contrast to investigating functional connectivity over time (e.g., [Fairhall and Ishai 2007](#)), we consider how these regions functionally coordinate over different tasks in response to their varied cognitive domains. Consistent with classic models ([Haxby et al. 2000](#)), we observed that functional coordination between core perceptual (OFA, FFA, and pSTS) regions was high. Interestingly, we observed that the fronto-lateral components of the classic extended system, IFG and OFC, coordinated more closely with these core regions rather than other elements of the classic extended system. It is notable that these fronto-lateral regions, particularly IFG, are closely related to extrinsic, task-activated, networks, distinguishing them from extended regions associated with the anticorrelated intrinsic resting state network ([Fox et al. 2005](#)). Additionally, during access to stored knowledge, the fronto-lateral IFG is implicated in guiding access to relevant information ([Martin and Chao 2001](#); [Wagner et al. 2001](#); [Thompson-Schill 2003](#)) suggesting a modulatory rather than representational role.

Other components of the extended system appear to coordinate most closely with each other across different cognition domains. Hierarchical clustering revealed an apparent dissociation between medial temporal components (ATFP and amygdala) and those associated with internalized cognition (vmPFC, precuneus, ATL, and AG). However, this was not confirmed by statistical analysis and future work will be needed to verify this grouping. A planned comparison of whether ATFP grouped more closely with core or extended systems revealed no evidence in either direction.

Cognitive Taxonomy in Person Knowledge

By considering the similarity between the neural profiles of different cognitive domains, we can gain insight into the relationship between these cognitive processes. We implemented this approach within the network for perceiving and knowing about others by comparing the profile of each task across the 21 ROIs comprising this network. We observed that for each task, despite variations in RTs and task structure, the 2 task-exemplars for each of the 5 cognitive domains reliably clustered with their counterpart. Demonstrating that cognitive domain is the primary grouping factor of activation patterns across this network and validating our selection of tasks. The general pattern of cognitive clustering across the regions suggests that social and physical knowledge share similar neural patterns, as do semantic and episodic knowledge, with nominal being represented somewhat distinctly. These findings fall broadly within hypothesized domain-specificity boundaries ([Spunt and Adolphs 2017](#)) suggesting that declarative memory (episodic and semantic tasks) and language (nominal tasks) are part of the “cognitive” macrodomain, while facial reception (physical tasks) and theory of mind (social tasks) are part of the “social” macrodomain.

Of specific interest to us was the relationship between episodic, semantic, and nominal knowledge. One classic distinction in forms of declarative memory is between episodic (personal experience) and semantic (general knowledge) ([Tulving 1972](#)). The term “semantic knowledge” refers to a broad range of knowledge about objects, factual knowledge,

and linguistic access to word meaning. Here we specifically contrasted competing models comparing whether semantic memory factual knowledge about people was more closely related to our personal experience and memories about that person than to access to their name, a task domain that strongly recruited language circuitry (see next section). Model comparison revealed significantly greater evidence that semantic memory clustered more closely to episodic than nominal access. This grouping is roughly apparent in the tuning profiles presented in Figure 3, where episodic and semantic domains load most heavily on regions associated with intrinsic cognition while nominal knowledge follows a different pattern—additionally engaging regions outside of the intrinsic network (e.g., IFG). In a broad sense, this result suggests that within the context of the tasks used in this study, semantic access shares a mechanism with episodic rather than linguistic neural systems.

Cognitive Domain Across the Whole Brain

In this study, we sought to understand how different elements of the person knowledge network, active spontaneously when we view familiar people (Gobbini and Haxby 2007), contribute to our diverse array of person-related knowledge. To this end, we perturbed the system toward 5 different cognitive domains to understand regional processing bias. However, these cognitive domains are not manifest solely within the person knowledge network, and a whole-brain analysis revealed cognitive domain-selective regions outside this network. Figure 6 shows the selective activation of cognitive domains across the brain (domain vs. others).

Recruitment of language regions in the nominal tasks: the supramarginal gyrus, lateral PFC, and dorsomedial PFC (Price 2012), validate the importance of linguistic processes in the performance of this task. Similarly, social knowledge tasks preferentially recruited regions of the left ATL and an anterior section of dorsomedial PFC, consistent with the social cognition network (Adolphs 2009). The engagement of broad parts of right lateral PFC as well as small clusters in medial temporal and occipital areas is consistent with the involvement of these regions in the retrieval of perceptual attributes (Kan et al. 2010). Episodic access generally recruited regions associated with autobiographical memory (Schacter et al. 2012; Spreng and Grady 2010). In particular, bilateral angular gyrus showed a strong modulation with episodic tasks and is an area associated with the strength of autobiographical recollection (Rissman et al. 2016). Notably, despite the involvement of a broad set of regions consistent with the episodic domain, the hippocampus was not recruited, even at uncorrected thresholds. The reason for this absence is uncertain but may relate to the use of a familiarity rather than recognition weighted tasks in our design (Eichenbaum et al. 2007) or due to low percentage of trials that loaded on episodic recollection. Collectively, these results indicate the separable nature of the cortical processes associated with these 5 cognitive domains and suggest that cognitive biases within the elements of the person knowledge network may arise from coordination with brain regions outside the network.

Conclusion

The current study examined how the distributed cortical network for perceiving and knowing about others coordinates to accomplish its diverse range of cognitive functions. By examining a range of tasks within a single study, we were able to observe

a clear preference for access to social over nominal knowledge in ATL and, within the TPJ, a clear division between a more perceptual pSTS and a more cognitively weighted angular gyrus—both in terms of their global response to cognitive access and the profile of activation across different cognitive domains. Through further multivariate analysis of the cognitive response profile across the network, we observed that regional coordination profiles grouped core regions with the lateral frontal extended system regions, which functioned relatively independently of intrinsic components of the extended system. Moreover, we were able to use similarity in activation patterns across the network to reconstruct a taxonomy that reflected how similar cognitive domains are to one another within the cortex. Notably, we observed that access to factual semantic knowledge employs neural substrates more similar to episodic memory than to language-related nominal knowledge. Collectively, these results demonstrate the importance of network-level dynamics in the instantiation of person-related cognition and knowledge. Future work will determine whether these principles extend to the representation of knowledge in general.

Data Availability

Binarized ROI mask (Table 3) and domain-specific t-statistic maps (Fig. 6 and Table 4) are freely available on NeuroVault (Gorgolewski et al. 2015) at the following URL: neurovault.org/collections/5362.

Funding

The project was funded by the European Research Council (ERC) grant CRASK - Cortical Representation of Abstract Semantic Knowledge, awarded to Scott Fairhall under the European Union's Horizon 2020 research and innovation program (grant agreement no. 640594).

References

- Adolphs R. 2002. Neural systems for recognizing emotion. *Curr Opin Neurobiol.* 12(2):169–177.
- Adolphs R. 2003. Cognitive neuroscience of human social behaviour. *Nat Rev Neurosci.* 4:165–178.
- Adolphs R. 2009. The social brain: neural basis of social knowledge. *Annual review of psychology.* 60:693–716.
- 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.
- Bortolon C, Capdevielle D, Raffard S. 2015. Face recognition in schizophrenia disorder: a comprehensive review of behavioral, neuroimaging and neurophysiological studies. *Neurosci Biobehav Rev.* 53:79–107.
- Bzdok D, Langner R, Caspers S, Kurth F, Habel U, Zilles K, Laird A, Eickhoff SB. 2010. ALE meta-analysis on facial judgments of trustworthiness and attractiveness. *Brain Struct Funct.* 215:209–223.
- Calder AJ, Young AW. 2005. Understanding the recognition of facial identity and facial expression. *Nat Rev Neurosci.* 6:641–651.
- Devlin JT, Russell RP, Davis MH, Price CJ, Wilson J, Moss HE, Matthews PM, Tyler LK. 2000. Susceptibility-induced loss of signal: comparing PET and fMRI on a semantic task. *Neuroimage.* 11:589–600.

- Downing PE, Peelen MV. 2011. How might occipitotemporal body-selective regions interact with other brain areas to support person perception? *Cogn Neurosci*. 2(3-4):216–226.
- Eichenbaum H, Yonelinas AP, Ranganath C. 2007. The medial temporal lobe and recognition memory. *Annu Rev Neurosci*. 30:123–152.
- 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. Category-selective neural substrates for person- and place-related concepts. *Cortex*. 49:2748–2757.
- Fairhall SL, Caramazza A. 2013b. Brain regions that represent amodal conceptual knowledge. *J Neurosci*. 33:10552–10558.
- Fairhall SL, Ishai A. 2007. Effective connectivity within the distributed cortical network for face perception. *Cerebral cortex*. 17(10):2400–2406.
- Fox MD, Snyder AZ, Vincent JL, Corbetta M, Van Essen DC, Raichle ME. 2005. The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proc Natl Acad Sci U S A*. 102:9673–9678.
- Frith CD. 2007. The social brain? *Philos Trans R Soc Lond B Biol Sci*. 362(1480):671–678.
- Gauthier I, Tarr MJ, Moylan J, Skudlarski P, Gore JC, Anderson AW. 2000. The fusiform “face area” is part of a network that processes faces at the individual level. *J Cogn Neurosci*. 12(3):495–504.
- Gesierich B, Jovicich J, Riello M, Adriani M, Monti A, Brentari V, Robinson SD, Wilson SM, Fairhall SL, Gorno-Tempini ML. 2011. Distinct neural substrates for semantic knowledge and naming in the temporoparietal network. *Cerebral Cortex*. 22(10):2217–2226.
- Glosser G, Salvucci AE, Chiaravalloti ND. 2003. Naming and recognizing famous faces in temporal lobe epilepsy. *Neurology*. 61:81–86.
- Gobbini MI, Haxby JV. 2007. Neural systems for recognition of familiar faces. *Neuropsychologia*. 45:32–41.
- Gorgolewski KJ, Varoquaux G, Rivera G, Schwarz Y, Ghosh SS, Maumet C, Sochat VV, Nichols TE, Poldrack RA, Poline JB et al. 2015. NeuroVault.org: a web-based repository for collecting and sharing unthresholded statistical maps of the human brain. *Front Neuroinform*. 9:8.
- Gorno-Tempini ML, Price CJ, Josephs O, Vandenberghe R, Cappa SF, Kapur N, Frackowiak RS, Tempini ML. 1998. The neural systems sustaining face and proper-name processing. *Brain*. 121(Pt 11):2103–2118.
- Grabowski TJ, Damasio H, Tranel D, Ponto LLB, Hichwa RD, Damasio AR. 2001. A role for left temporal pole in the retrieval of words for unique entities. *Hum Brain Mapp*. 13:199–212.
- Greene JD, Sommerville RB, Nystrom LE, Darley JM, Cohen JD. 2001. An fMRI investigation of emotional engagement in moral judgment. *Science*. 293:2105–2108.
- Haxby JV, Hoffman EA, Gobbini MI. 2000. The distributed human neural system for face perception. *Trends Cogn Sci*. 4:223–233.
- Von Der Heide RJ, Skipper LM, Olson IR. 2013. Anterior temporal face patches: a meta-analysis and empirical study. *Front Hum Neurosci*. 7:17.
- Hein G, Knight RT. 2008. Superior temporal sulcus—it’s my area: or is it? *J Cogn Neurosci*. 20(12):2125–2136.
- Huth AG, de Heer WA, Griffiths TL, Theunissen FE, Gallant JL. 2016. Natural speech reveals the semantic maps that tile human cerebral cortex. *Nature*. 532:453–458.
- Kan IP, Barsalou LW, Solomon KO, Minor JK, Thompson-Schill SL. 2010. Role of mental imagery in a property verification task: fmri evidence for perceptual representations of conceptual knowledge. *Cogn Neuropsychol*. 20:525–540.
- Kanwisher N, McDermott J, Chun MM. 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J Neurosci*. 17:4302–4311.
- Keidel JL, Oedekoven CS, Tut AC, Bird CM. 2017. Multiscale integration of contextual information during a naturalistic task. *Cerebral Cortex*. 28(10):3531–3539.
- Koster-Hale J, Richardson H, Velez N, Asaba M, Young L, Saxe R. 2017. Mentalizing regions represent distributed, continuous, and abstract dimensions of others’ beliefs. *Neuroimage*. 161:9–18.
- Martin A, Chao LL. 2001. Semantic memory and the brain: structure and processes. *Curr Opin Neurobiol*. 11:194–201.
- Minnebusch DA, Daum I. 2009. Neuropsychological mechanisms of visual face and body perception. *Neurosci Biobehav Rev*. 33:1133–1144.
- Moeller S, Freiwald WA, Tsao DY. 2008. Patches with links: a unified system for processing faces in the macaque temporal lobe. *Science*. 320:1355–1359.
- Moran JM, Lee SM, Gabrieli JD. 2011. Dissociable neural systems supporting knowledge about human character and appearance in ourselves and others. *Journal of cognitive neuroscience*. 23(9):2222–2230.
- Murray RJ, Schaer M, Debbane M. 2012. Degrees of separation: a quantitative neuroimaging meta-analysis investigating self-specificity and shared neural activation between self- and other-reflection. *Neurosci Biobehav Rev*. 36(3):1043–1059.
- Olson IR, McCoy D, Klobusicky E, Ross LA. 2013. Social cognition and the anterior temporal lobes: a review and theoretical framework. *Soc Cogn Affect Neurosci*. 8:123–133.
- Olson IR, Plotzker A, Ezzyat Y. 2007. The enigmatic temporal pole: a review of findings on social and emotional processing. *Brain*. 130:1718–1.
- 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.
- Price CJ. 2012. A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. *Neuroimage*. 62:816–847.
- Raichle ME, MacLeod AM, Snyder AZ, Powers WJ, Gusnard DA, Shulman GL. 2001. A default mode of brain function. *Proc Natl Acad Sci U S A*. 98:676–682.
- Rajimehr R, Young JC, Tootell RBH. 2009. An anterior temporal face patch in human cortex, predicted by macaque maps. *Proc Natl Acad Sci U S A*. 106:1995–2000.
- Rissman J, Chow TE, Reggente N, Wagner AD. 2016. Decoding fMRI signatures of real-world autobiographical memory retrieval. *J Cogn Neurosci*. 28(4):604–620.
- Ross LA, Olson IR. 2011. What’s unique about unique entities? An fMRI investigation of the semantics of famous faces and landmarks. *Cerebral Cortex*. 22(9):2005–2015.
- Saxe R, Powell LJ. 2006. It’s the thought that counts: specific brain regions for one component of theory of mind. *Psychol Sci*. 17:692–699.
- Schacter DL, Addis DR. 2007. The cognitive neuroscience of constructive memory: remembering the past and imagining the future. *Philos Trans R Soc Lond B Biol Sci*. 362:773–786.
- Schacter DL, Addis DR, Hassabis D, Martin VC, Spreng RN, Szpunar KK. 2012. The future of memory: remembering, imagining, and the brain. *Neuron*. 76(4):677–694.

- Semenza C. 2011. Naming with proper names: the left temporal pole theory. *Behav Neurol.* 24:277–284.
- Simmons WK, Martin A. 2009. The anterior temporal lobes and the functional architecture of semantic memory. *J Inter Neuropsychol Soc.* 15:645.
- Spreng RN, Stevens WD, Chamberlain JP, Gilmore AW, Schacter DL. 2010. Default network activity, coupled with the frontoparietal control network, supports goal-directed cognition. *Neuroimage.* 53:303–317.
- Spreng RN, Grady CL. 2010. Patterns of brain activity supporting autobiographical memory, prospection, and theory of mind, and their relationship to the default mode network. *J Cogn Neurosci.* 22(6):1112–1123.
- Spunt RP, Adolphs R. 2017. A new look at domain specificity: insights from social neuroscience. *Nat Rev Neurosci.* 18:559–567.
- Thompson-Schill SL. 2003. Neuroimaging studies of semantic memory: inferring “how” from “where”. *Neuropsychologia.* 41:280–292.
- Tippett LJ, Miller LA, Farah MJ. 2000. Prosopamnesia: a selective impairment in face learning. *Cogn Neuropsychol.* 17:241–255.
- Todorov A, Gobbini MI, Evans KK, Haxby JV. 2007. Spontaneous retrieval of affective person knowledge in face perception. 45:163–173.
- Tulving E. 1972. Episodic and semantic memory. *Organization of memory.* New York, NY: Academic Press, Vol 1, pp. 381–403.
- Van Overwalle F. 2009. Social cognition and the brain: a meta-analysis. *Hum Brain Mapp.* 30:829–858.
- Van Overwalle F. 2011. A dissociation between social mentalizing and general reasoning. *Neuroimage.* 54:1589–1599.
- Viard A, Chételat G, Lebreton K, Desgranges B, Landeau B, La Sayette de V, Eustache F, Piolino P. 2011. Mental time travel into the past and the future in healthy aged adults: an fMRI study. *Brain Cogn.* 75:1–9.
- Wagner AD, Paré-Blagoev EJ, Clark J, Poldrack RA. 2001. Recovering meaning: left prefrontal cortex guides controlled semantic retrieval. *Neuron.* 31(2):329–338.
- Werner NS, Kühnel S, Markowitsch HJ. 2013. The neuroscience of face processing and identification in eyewitnesses and offenders. *Frontiers in behavioral neuroscience.* 7:189.
- Wieser MJ, Brosch T. 2012. Faces in context: a review and systematization of contextual influences on affective face processing. *Frontiers in psychology.* 3:471.