

Regional Specialisation and Coordination within the Network for Perceiving and Knowing about
Others

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Aidas Aglinskas and Scott L. Fairhall

Abstract

Seeing familiar faces prompts the recall of diverse kinds of person-related knowledge. How this information is encoded within the well-characterised face/person selective network is a complex and outstanding question. To address this issue, we had participants access five different kinds of person knowledge (social, episodic, semantic, physical, nominal) through ten different experimental tasks. By directly comparing different cognition domains, we are able to: 1) test the relative roles of brain regions in specific cognitive processes, such as the role of ATL in social or nominal knowledge and 2) apply a multivariate Network-level Representational Similarity Analysis (netRSA) to gain insight into underlying systems-level organisation of the person-knowledge network. NetRSA revealed a strong divide between regions involved in internalised cognition (precuneus, mPFC, ATL etc.) and other elements of the person-knowledge network. Fronto-lateral regions (IFG and OFC) coordinate closely with perceptual regions in the core system (FFA, OFA, pSTS). NetRSA also revealed a taxonomy of cognitive processes, with semantic retrieval being more similar to episodic than nominal knowledge and distinct from social and physical knowledge. Collectively these results demonstrate how coordinated activity across core-extended divisions of the person knowledge network enact the diverse cognitive capacities of this system.

Keywords: cortical network, face perception, fMRI, representational similarity analysis, semantics.

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, Hoffman, and Gobbini 2000; Gobbini and Haxby 2007; Fairhall and Ishai 2007). This network is composed of a perceptual 'core system', the occipital and fusiform face areas (OFA, 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, Hoffman, and Gobbini 2000). The extended system includes lateral frontal regions: inferior frontal gyri (IFG), lateral orbitofrontal cortex (OFC); regions associated with internalised cognition: the anterior temporal lobes (ATL), precuneus, ventromedial and dorsomedial prefrontal cortices (vmPFC, dmPFC); and medial temporal regions: the amygdalae and potentially the recently identified anterior temporal face patch ATFP (Moeller et al. 2008; Rajimehr et al. 2009).

Numerous investigations of the contribution of these regions have produced diverse, and at times discordant, results (Table 1). For example, while the pSTS is classically characterised 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 (Simmons and Martin 2009) illustrate further the diversity and complexity of regional roles within the extended system.

Much insight has been gained from research addressing single cognitive function in one or a few brain regions. However, this approach has the potential to ambiguate the true regional functions of regions**. Ambiguities surrounding regional function are expounded by the tendency of research to address single cognitive functions in one or a few brain regions. 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 internalised cognitive processes (Spreng et al. 2010). These include not only the eponymous 'default mode', task-deactivated states (Raichle et al. 2001) but also a broad range of internalised cognitive processes: general semantic knowledge (Binder et al. 2009; Fairhall and Caramazza 2013b; Huth et al. 2016); 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, Oedekoven, Tut & Bird, 2017). As elements of the internalised 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. Then we push the network towards different aspects of person knowledge (social, semantic, episodic, nominal and physical) to understand the relative importance of these processes to each region. The goals of the current experiment are twofold. 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 anterior temporal lobe 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 two questions: a) how are cognitive domains represented across the network and b) how do these regions work together to accomplish the diverse range of ensemble functions of the network. We hypothesise 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.

Table 1. illustrates complex cognitive landscape of the attribution of cognitive roles to various regions of the person-knowledge network. We sampled published reviews and meta-analyses reporting regional function in in the context of person perception of knowledge. Attributions have been broadly grouped into the categories such as Perception, Semantic knowledge, or Working memory.

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 & 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)
vmPFC	Social knowledge & personality traits (Adolphs 2003; Adolphs:2002wo Werner et al. 2013) Mental states (Gobbini and Haxby 2007; Wieser and Brosch 2012) Emotion (Werner et al. 2013) Attractiveness & 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)
	Perception (Adolphs 2003)
pSTS	Social knowledge & Mental states (Gobbini and Haxby 2007; Wieser and Brosch 2012)
	Emotion (Gobbini and Haxby 2007)
Amygdala	Physical knowledge (Bzdok et al. 2010)
	Social knowledge (Bzdok et al. 2010)
	Familiarity (Ross and Olson 2012; Heide et al. 2013)
ATFP	Identity representation (Ross and Olson 2012)

Methods

Participants

Twenty right-handed, native Italian participants (8 males; mean age: 23.2 years, range: 19-32 years) took part in this study. 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 centred on the screen (1280x1024 resolution, 60hz refresh rate), with grey background. After the experiment 13/20 participants were presented with faces they saw in the experiment and asked whether they recognised the celebrity. On average, the subjects recognised $M = 84\%$ of faces.

Task

Each experimental block started with 4s instruction screen specifying the task, followed by 6s of fixation cross. After that a face was presented for .5s followed by 2s 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 five categories of person knowledge: episodic memories, semantic knowledge, social judgments, nominal knowledge and physical knowledge. For each of the categories, we chose two different probe questions that require access to each kind of knowledge (totalling ten experimental tasks; see Figure 1 and Table 2). In addition, there were two 1-back matching control tasks with either pictures of faces or famous monuments. The experiment consisted of five runs (8 min, 42s each). Sixteen blocks were presented in a randomised order (one block for each task plus three face and three monument 1-back control blocks).

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

Knowledge category	Task	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)
Perceptual	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?	<i>How familiar is this person is for you?</i>	Likert scale (1-4)
	First memory?	<i>For how long have you known this person?</i>	Likert scale (1-4)
Semantic	How many facts?	How many facts could you recall about this person?	Likert scale (1-4)
	Job?	What is this person occupation?	Predefined categories (see 'task')

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

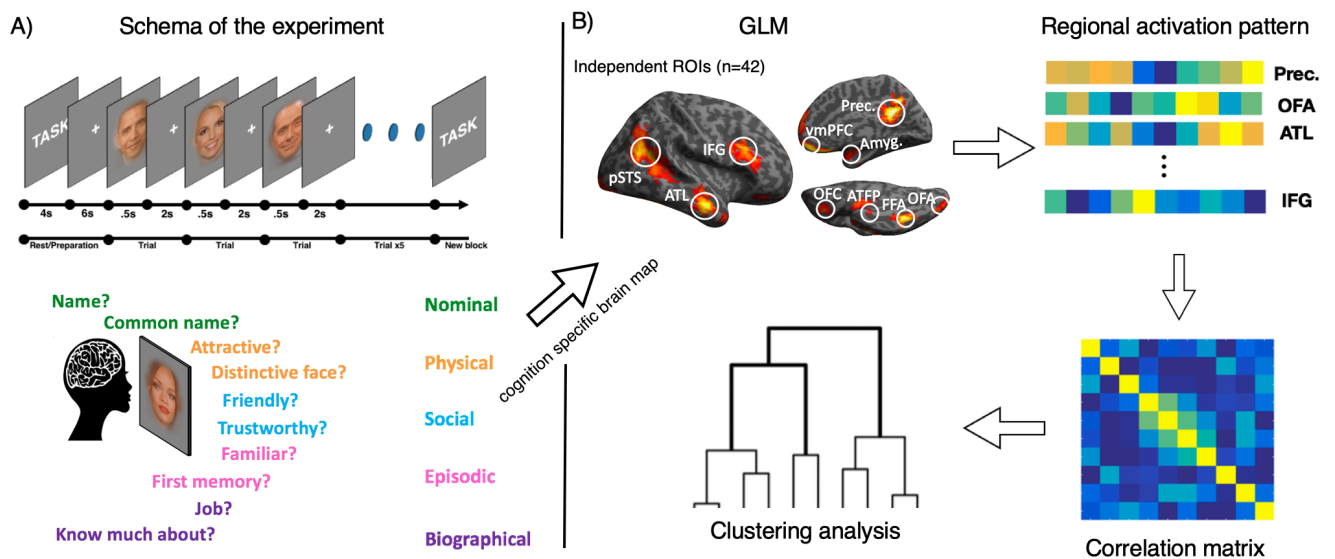


Figure 1. (A) Top: Schematic representation of the experiment. Experimental blocks were preceded by 4s of instruction screen, and 6s fixation point. Each trial consisted of .5s face presentation and 2s fixation. Bottom: five domains of person knowledge and two questions per domain are noted in corresponding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

[add 'task→' to top right panel].

['correlation matrix' might be a bit vague]

Data Acquisition

Participants were scanned at the Center for Mind/Brain Sciences (CIMEC), University of Trento, Italy. Data was collected using Bruker BioSpin MedSpec 4T, with 8-channel phased-array head coil. Five runs of 209 echo-planar volumes, consisting of 34, AC-PC aligned axial slices were acquired while participants performed the task (FOV = 64mm x 64mm, TR = 2.5s, TE = 33, FA = 73°). Voxel size was 3x3x3mm with a 1mm gap. In addition to functional data, a whole brain T1 MPRAGE anatomical image was acquired (whole brain (FOV = 256x224, 176 1mm axial slices).

Region of interest definition

Regions of interest (ROIs) were selected from an independent (N=42) experiment, conducted for high power functional localisation. In the localiser experiment participants performed a 1-back matching task with 12 second blocks of famous faces, common animals or common objects. The contrast faces > animals+tools ($p < .05$ FWE corrected) was used to identify face selective peaks (Table 2). 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.

Table 3: ROI sphere centre coordinates. Peak coordinates for regions active in the localiser experiment (N=42) and ROI sizes in voxels after thresholding. Coordinates are in MNI space.

Region	Hemisphere	X	Y	Z	ROI size
Precuneus	Medial	3	-52	29	81
OFA	Right	30	-91	-10	65

	Left	-33	-88	-10	49
FFA	Right	42	-46	-22	81
	Left	-39	-46	-22	30
IFG	Right	39	17	23	44
	Left	-36	20	26	38
ATL	Left	-60	-7	-19	69
	Right	57	-7	-19	81
Amygdala	Left	-21	-10	-13	62
	Right	21	-7	-16	59
dmPFC	Medial	6	59	23	59
vmPFC	Medial	3	50	-19	66
OFC	Right	33	35	-13	58
	Left	-33	35	-13	27
ATFP	Right	33	-10	-40	39
	Left	-36	-10	-34	24
Angular	Left	-48	-67	35	68
	Right	42	-64	35	57
pSTS	Left	-48	-49	14	54
	Right	48	-55	14	71

Data Analysis

Data were pre-processed with SPM12. Functional images were realigned to account for motion, grey matter segmented, warped into common space and smoothed with 8mm FWHM kernel. Subject specific response estimates (beta weights) were derived by fitting a general linear model (GLM) to the data. 12 regressors (10 tasks, 2 controls) were included as explanatory variables. Six motion parameters from re-alignment procedure were included as regressors of no interest. We drew 7.5mm spheres around chosen coordinates (Table 2) and extracted the mean beta value significantly active at $p < 0.001$ within those ROIs (contrast faces > animals+tools). To isolate the

magnitude of cognitive response, we subtracted beta value for 1-back matching face control task from each experimental task.

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

Behavioural Data

Mean Reaction time (RT) was $M = 1203$ msec, $SD = 111$ msec. 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 ten tasks ($F(9, 171) = 17.13$, $p < .001$). Critically, this RT effect did not persist when tasks were collapsed into the five domains of knowledge used in the imaging analysis (i.e. “Nominal“, “Physical“, “Social“, “Episodic“, “Semantic“; $F(4, 95) = 2.21$ $p = .076$). RT did not significantly differ between face ($M = .71$, $SD = .11$) and place ($M = .68$, $SD = .12$) control 1-back matching tasks ($t(18) = 1.96$, $p = .066$).

Mean ratings ranged from $M = 2.2$, $SD = 0.25$ (attractiveness task) to $M = 3.1$, $SD = .38$ (full name task). Ratings differed across 10 exemplar tasks ($F(4.8, 91.7) = 27.741$, $p < .001$, Greenhouse-Geisser correction) and 5 cognitive domains ($F(4,76) = 20.03$, $p < .001$). Faces were rated highest on attractiveness ($M = 2.79$, $SD = .025$) and lowest on participants' ability to recall full name ($M = 1.82$, $SD = .38$). To check whether task ratings influence task representation in the

brain, we constructed RSA 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 ($t(19) = .78$. $p = .442$).

Role of regions in access to person knowledge.

Extended but not core regions show an increased response during access to person knowledge.

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 one-back matching task on famous faces. The results are shown in Figure 2.

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[why only single asterisks?]

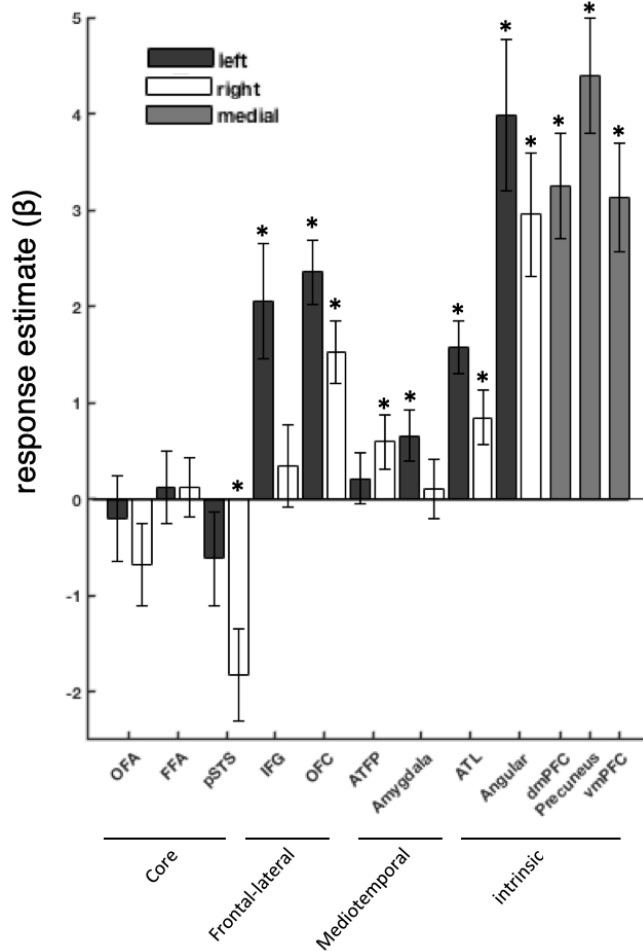


Figure 2: Regional response to person knowledge access (average of experimental tasks > face control task). Bars show response estimate magnitude (beta value), error bars represent standard error of the mean (SE). Retrieving person knowledge activated extended system regions to variable extent, but core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

Could we maybe space out the sub-networks (I want it visually clear that the core is down, frontolateral is up etc, and it is not at the moment)

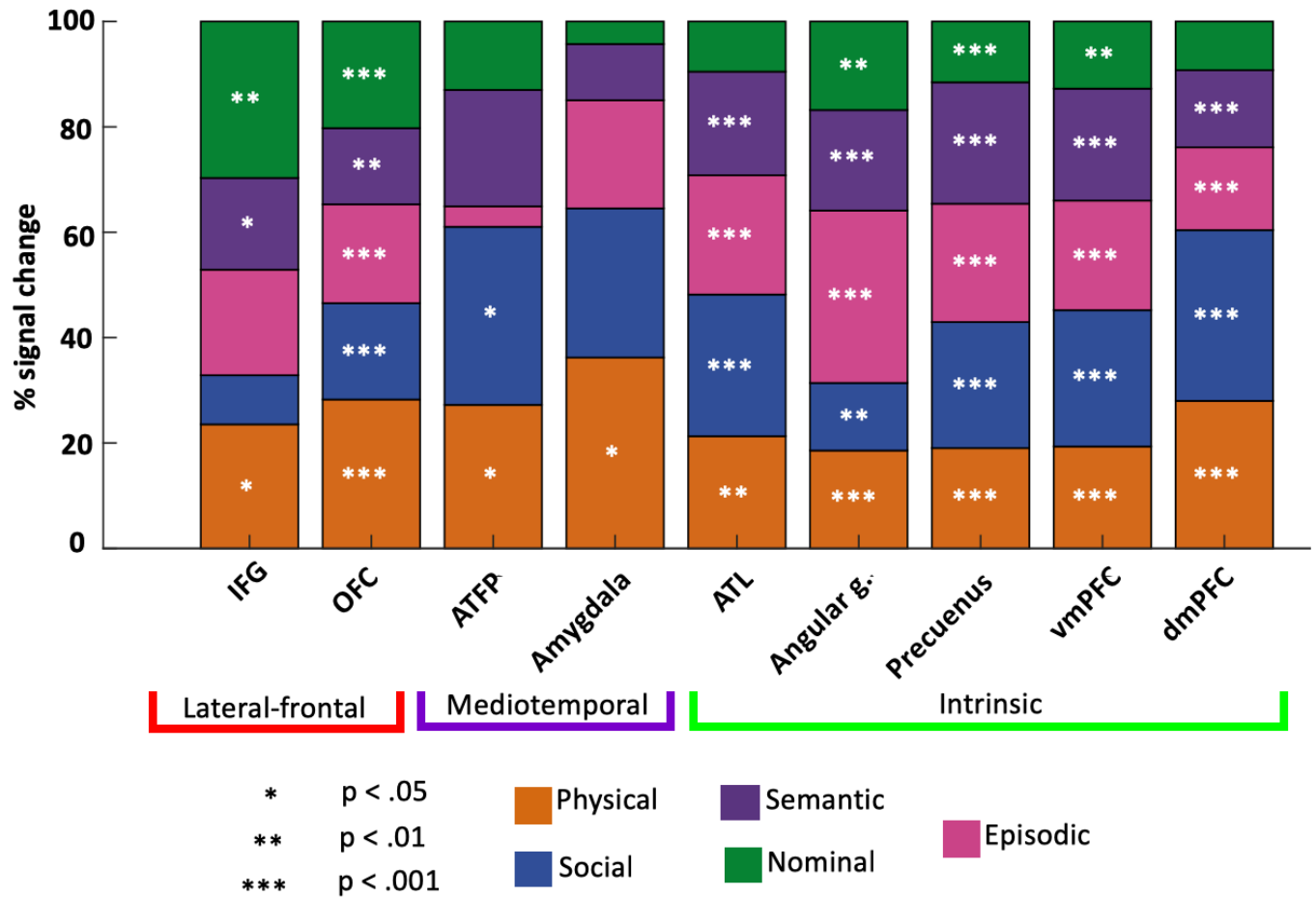
The most apparent distinction is between regions of the core system, which show no increase in activity ($t(19) = -1.69, p = .11$; averaged across all core regions) and other elements of the network ($t(19) = 6.98, p < .001$; averaged across all extended regions). A second clear

organisational feature of person knowledge is the left lateralisation of this process, with left hemisphere regions showing a greater relative increase when accessing person knowledge than their right hemisphere counterparts ($t(19) = 4.67, p < .001$).

Individually, regions of the internalised cognition part of extended system were all strongly recruited during access to person knowledge (t -values > 4.60 , p -values $< .001$). 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. 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; $F(4,76) = 2.508, p = 0.49$ [.049, right?]). 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.



[asterisk are still not centred.] [lateral-frontal axis label seems uncentered] [labels for cog domain are un-aligned] Figure 3. Regional preference patterns. Percentage of total activation elicited by each cognitive domain. Stars denote significance threshold. Most regions are involved in most cognitive domains. Although patterns vary across components of the network, it can also be seen that regions that respond to episodic knowledge tend to respond to semantic access as well.

The ATL is weighted towards 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. ANOVA revealed significant differences across cognitive domains ($F(4, 95) = 8.13, p < .001$). A planned comparison specifically testing the role of social and nominal tasks revealed that access to social knowledge recruited this region to a greater extent than access to nominal knowledge ($t(19) = 5.79, p < .001$), with nominal knowledge showing no significant increase compared to control ($t(19) = 2.08, p = .052$). 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 -values > 2.49 , all p -values $< .02$, uncorrected). The response during the nominal tasks were not diminished in all regions, with IFG responding more strongly to access to nominal than social knowledge ($t(19) = 3.1, p = .006$). 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 non-perceptual 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 knowledge retrieval.** The functional division between these two regions was apparent even at a level of global access to person-knowledge, (c.f. figure 2). Specifically, while the pSTS showed a suppressed response during access to stored person-knowledge (pSTS left: $t(19) = -1.26, ns.$; right: $t(19) = -3.81, p = .001$), the angular gyrus conversely showed a robust response (AG left: $t(19) = 5.81, p < .001.$; right: $t(19) = 2.99, p = .008$). This difference was also apparent in the global laterality pattern. pSTS showed a stronger inhibition in response on the right ($t(19) = 3.47, p = .001$), consistent

with the pattern of right laterality in core regions. Conversely, there was no laterality effect in global response of the angular gyrus ($t(19) = 1.57, p = .134$). Collectively, these patterns underscore the pronofunctional subdivision of these regions of the temporo-parietal junction.

At the level of the single cognitive domain (see Figure 3) an increased response in AG was evident across each cognitive domain ($t > 3.12, p < .006$) while the pSTS did not show and 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 ($t > 2.8, p < .01$). Together, these results demonstrate a pattern of response in the pSTS consistent with core perceptual processing and a pattern in the AG consistent with access to knowledge. Differences in inter-regional coordination patterns will be discussed in the next section.

Inter-Regional Coordination and Network organisation

Which brain regions work together to accomplish the person-knowledge network's varied functions? The functional coordination between ROIs was examined through a network level Representational Similarity Analysis (*netRSA*). The ten task-induced beta patterns were correlated between each pair of ROIs and subjected to hierarchical clustering analysis (see figure 1 and methods). The validity of this netRSA approach is confirmed by the close proximity of left and right regional homologues (figure 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 (figure 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 homologues despite hemispheric asymmetries in the overall response.

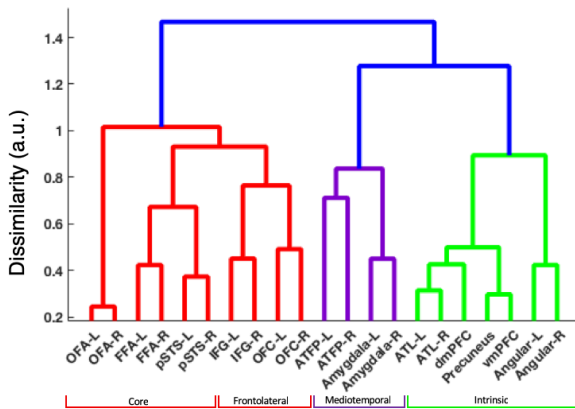
At a descriptive level, netRSA revealed the expected cognitive clustering of core regions (OFA, FFA, pSTS). Interestingly, the lateral frontal regions the orbito-frontal and inferior frontal

gyri cluster with the core system, rather than the other components of the extended system (figure 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 figure 4). Post hoc comparisons of the goodness of fit between the two competing models confirmed that lateral frontal regions co-ordinate more closely with core than other extended system regions ($t(19) = 3.09$, $p = .006$). Considering regions separately, this effect persisted for IFG ($t(19) = 4.35$, $p < 0.001$), while no preference was evident for OFC ($t(19) = 1.59$, $p = 0.13$).

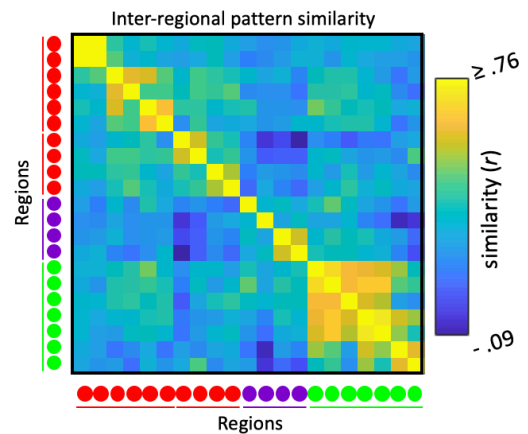
Within the extended system, regions overlapping with those associated with internalised cognition form a distinct cluster (Cluster 2 - green) with respect to the amygdala and anterior face patch of the medial temporal lobe (Cluster 3 – purple). However, planned comparison of whether the ATFP groups more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

Network organisation: regional pattern similarity

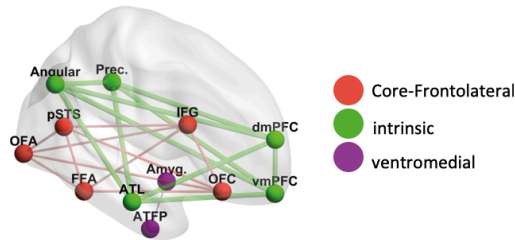
A) Hierarchical clustering



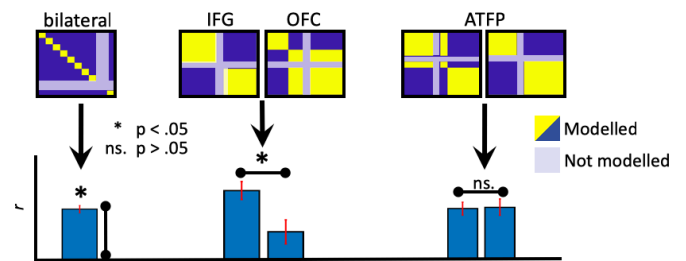
C) Model comparison



B) Anatomical schematic of network connections



Network organisation models



[straighten colourbar labels] [use more asterisks to indicate robustness of significance]

[make blue line in A) black] [the IFG and OFC labels on the network organisation models confused me].

[Y-label on model evidence] *Figure 4. A) ROI clustering. First major division separates core together with IFG & 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, green). B) Schematic representation of clusters projected onto the brain. C) model comparison schematic. Competing models of network organisation were constructed, fitted to observed data for each participant, and compared in a paired samples t-test.*

Cognitive Domain Similarity in the Brain

Cortical Similarity between Cognitive Domains

Cognitive Domain Similarity in Cortical Profile**cognitive taxonomy grounded in brain representation.**

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 Figure 5 and methods). Despite variance across tasks, reaction times, 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 ($t(19) = 4.14, p < 0.001$).

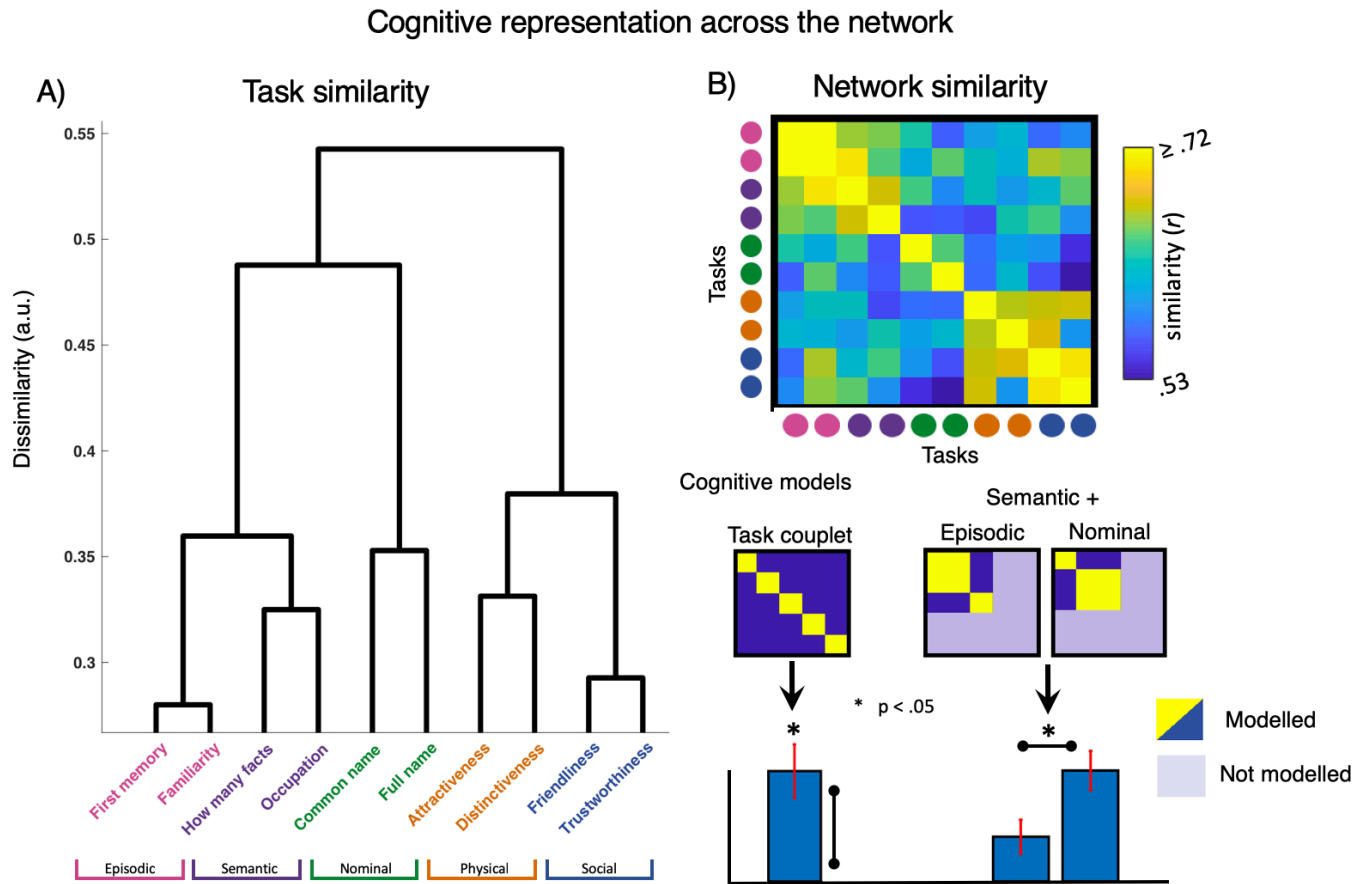


Figure 5. A) [random bar for ‘task couplet bar plot- either shift the asterisk of kill the bar]] Task similarity in core and extended system ROIs. Tasks are grouped according to the domain they were sampled from. Episodic and semantic knowledge retrieval tasks elicit differentiable patterns from nominal, physical or social ones (dendrogram, left). B) fMRI pattern similarity matrix and models tested. [change range for b to .5 – .75.] [could add ***s to indicate greater significance]

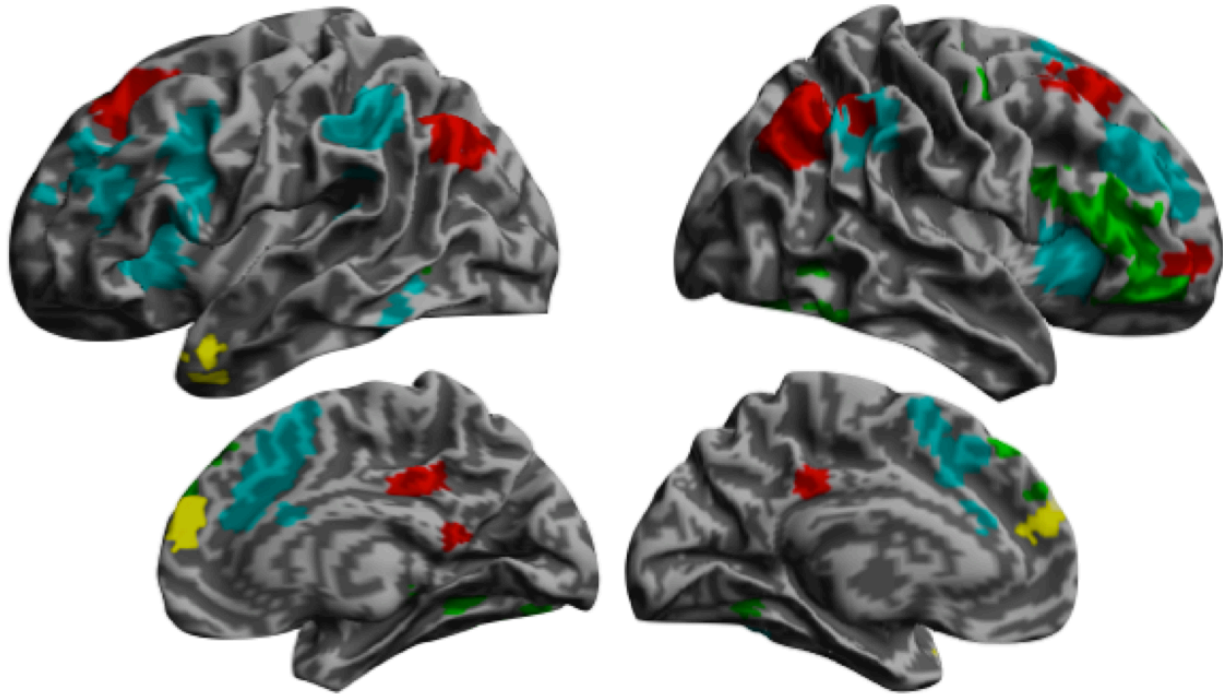
At the next level of hierarchical clustering, results reveal three distinct cognitive clusters. Network activity is more similar for physical (yellow) and social (blue) knowledge than to other forms of knowledge. Likewise, episodic (pink) and semantic (purple) knowledge form a cluster, that is distinct from nominal knowledge. We compared competing models (see Figure 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 ($t(19) = 3.97, p < .001$).

Whole Brain Analysis - Beyond the person-selective network

The motivation of this project was to gain insight into the normal function of the well-characterised network for person knowledge by strongly pushing the system towards access to different domains of knowledge. While we focus on the network for perceiving and knowing about others, cognitive processes are not enacted solely by the person knowledge system. It is important to consider that these systems presumably pair and couple with brain regions outside the person-selective network, with the network's periphery potentially driving transient specialisation 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 two or more cognitive domains, consistent with non-overlapping cognitive specialisation outside the person knowledge network. Access to nominal knowledge is characterised by a broad pattern of activation, stronger in the left hemisphere than the right (Figure 6, Table 4). It encompasses left hemispheric sites associated with language production [reference?]and comprehension, as well as the posterior middle/inferior temporal gyrus [is this region not associated with language comprehension?]. 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. Semantic knowledge retrieval tasks did not selectively recruit any region outside of the person-knowledge network.



$p < .001$ (voxel); $p < .05$ (FWE, cluster corrected)

■ Nominal **■ Physical** **■ Social** **■ Episodic**

[BIGGER] Figure 6. Cognition specific brain activations. Whole brain map highlights peripheral, domain specific cognitive systems that are recruited during diverse kinds of person-knowledge retrieval. 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: Figure 6). SFG - superior frontal gyrus, IPL - inferior parietal lobule. PMC - premotor cortex, PCC – posterior cingulate cortex..

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
Physical	IFG	Right	< 0.001	616	5.72
	FFA	Right	< 0.001	274	4.86
	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
Nominal	IFG	Left	< 0.001	1188	6.99
	SFG	Medial	< 0.001	1670	6.40
	Angular	Left	< 0.001	370	6.35
	Angular	Right	< 0.001	265	5.31
	FFA	Left	0.003	97	4.70

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 inter-regional coordination that endow distributed cortical networks their considerable cognitive flexibility. By relating task activity not only to a baseline but 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 organisation, 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.

***Even at the broadest level we see a clear division between core and extended system regions. Face-selective core system regions (OFA, FFA & 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, Hoffman, and Gobbini 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 gyral 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 ~~supports the reclassification of 'pSTS' into face-selective pSTS and person-selective angular gyrus and~~ 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 non-visual theory of mind (Saxe and Powell 2006) and amodal access to person knowledge (Fairhall and Caramazza 2013b) and a pSTS component involved in face perception. [** This should be 2013*a* **] 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 two 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 the 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 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 generalised 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 three domains, the whole brain analysis (Figure 6) only social knowledge showed a significant cognitive selective response in adjacent the left ATL, consistent with the importance of social knowledge in this region.*

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, Hoffman, and Gobbini 2000b) 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 anti-correlated 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, amygdala) and those associated with internalised cognition (vmPFC, precuneus, ATL, 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 profile 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 reaction times and task structure, that the two task-exemplars for each of the five 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 perceptual knowledge share similar neural patterns, as do semantic and episodic knowledge with nominal being represented somewhat distinctly. These findings fall broadly within hypothesised domain-specificity boundaries (Spunt and Adolphs 2017) suggesting that declarative memory (episodic, semantic tasks) and language (nominal tasks) are part of the 'cognitive' macro-domain, while facial reception (physical tasks) and theory of mind (social tasks) are part of the 'social' macro-domain. 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 components comparing whether semantic memory in the form of factual knowledge about people was more closely related to our personal experience and memories about that person than 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 topography - engaging mainly parts of the intrinsic network as well as regions outside of it (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 the 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 towards five 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 the cognitive-domain selective regions outside this network. Figure X shows the selective activation of cognitive domains across the brain (domain v. others).

Recruitment of language regions in the Nominal task: 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, Neuron; Spreng and Grady, (2009), 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, JCON). However, despite distinct 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 task (Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The medial temporal lobe and recognition memory. *Annu. Rev. Neurosci.*, 30, 123-152.) in our design or to other factors related to this kind of episodic access.

Collectively, these results indicate the separable nature of the cortical processes associated with our five cognitive domains and emphasises the coordination of regions of the person knowledge network with other brain regions in the perform of their tasks [poorly worded].

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 a clear division between a more perceptual pSTS and a more

cognitive angular gyrus components of TPJ, 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 reconstruct a taxonomy that reflected how cortically similar cognitive domains are to one another. 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.

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