SPECIAL ISSUE

Features, labels, space, and time: Factors supporting taxonomic relationships in the anterior temporal lobe and thematic relationships in the angular gyrus

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Features, labels, space, and time: Exploring taxonomic and thematic semantic relationships in the anterior temporal lobe and angular gyrus

Having the concept coffee involves knowing not only how coffee looks, smells, and tastes, but also how it *relates* to other things. We consider two types of conceptual relationships: (1) taxonomic, i.e., between entities that share multiple features (e.g. coffee–tea), and (2) thematic, i.e., what things 'go together' in an event (e.g. coffee–spoon). We first review data suggesting that taxonomic and thematic relations are supported by semantic 'hubs' in the anterior temporal lobe (ATL) and angular gyrus (AG), respectively. We then propose that the AG's connectivity to hippocampal regions supports its sensitivity to episodic detail and hence the event structures and context-sensitivities characterizing thematic relations, and that ATL's connectivity with perirhinal cortex, which supports discrimination, promotes taxonomic categorization. Finally, we discuss several reasons that labelling may be particularly critical for taxonomic relations, and propose that processing in ATL is influenced by labels because of connectivity with frontal language regions.

Keywords: concepts, semantic memory, taxonomic, thematic

Introduction

Humans operate in their worlds in large part by creating and making use of concepts. Upon smelling *coffee* for instance, we can make good guesses (or predictions) about its other properties, such as its taste. Or, if we discover that we're out of coffee, we may opt for a related beverage like tea. We also have knowledge about the contexts in which things are likely to appear, and how they are used in conjunction with other things. For instance, we may head for the fridge to fetch the milk before pouring our coffee, knowing that milk and coffee are used together. And before fetching the milk, we may retrieve a spoon from the drawer in anticipation of stirring in the milk. Each of these activities requires conceptual knowledge – to understand what coffee is, how it is instantiated in different forms, how it relates to other beverages like tea, as well as the sorts of things we do and use along with our coffee (or tea), like a spoon, sugar, milk, and mug.

To account for some of this conceptual knowledge, and in particular, to account for how we know what is similar to what (e.g. that coffee is similar to tea), many cognitive neuroscientifically oriented perspectives on concept representation propose some sort of 'hub' system. A prominent 'hub-based' theory, the distributed-plus-hub model (for reviews, see Lambon Ralph, 2014; Patterson, Nestor, & Rogers, 2007; for recent extensions, see Chen, Lambon Ralph, & Rogers, 2017; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017), suggests that modality-specific featural information that is distributed across cortex (e.g. features such as the colour of coffee in visual cortex, and its distinct smell in the olfactory system) converges in a hub. Via sensitivity to statistical regularities between these features, we are able to create or 'abstract' representations that reflect a particular thing or class of things (defined through sharing those statistical tendencies, e.g. dark coloured, hot, and tastes and smells a particular way). When we experience something new, its features are analysed with respect to the similarity space housed in the hub – if the new experience shares attributes with a previously abstracted concept, this new experience will inherit statistical tendencies from the previously formed concept. In other words, attributes from the previously formed concept will be 'generalized' to the new one. For instance, even if tea were entirely new to us, experiencing the many shared features among coffee and tea would allow us to generalize from our experiences with coffee to the likely effects of tea (e.g. stimulation, a warming sensation).

The distributed-plus-hub model successfully explains several phenomena pertaining to the acquisition and deployment of conceptual knowledge, including how a hub could allow *coffee* and *tea* to come to be related to each other while remaining distinct from objects like cups and canisters (e.g. Rogers et al., 2004). It also offers a candidate brain region for the hub, the anterior temporal lobe (ATL), and successfully predicts that damage to this region will lead to an inability to recognize *coffee* regardless of whether it is presented visually, smelled, or tasted, and an inability to draw relations between categorically related concepts like coffee and tea (Rogers et al., 2004). Yet, while the distributed-plus-hub view provides a compelling account for one important aspect of our conceptual knowledge (i.e. how we know what kind of thing something is and what it is similar to, also called *taxonomic* knowledge), it does not account for the other critical aspect of our conceptual knowledge introduced above – that spoon, milk, cup, and canister are also part of our *coffee* concept. In other words, it does not account for how we know what things go together, and the contexts in which they are likely to do so. This latter type of conceptual knowledge is often called *thematic* knowledge (for a review, see Estes, Golonka, & Jones, 2011).

This has led some to argue that the conceptual system might be better characterized by two hubs: a taxonomic hub, situated in the ATL, which supports relations between things that share multiple features (e.g. coffee and tea), thus allowing for identification (e.g. that warm, black, fragrant liquid is coffee) and categorization (e.g. coffee and tea are both beverages); and a thematic hub, situated in the angular gyrus (AG) that broadly supports event-based relations, and thus supports associations (e.g. coffee comes in a mug) and predictions about what might come next (e.g. I may add milk to my coffee and stir it with a spoon; for review, see Mirman, Landrigan, & Britt, 2017; Schwartz et al., 2011).

This idea, that taxonomic and thematic knowledge systems are dissociable and supported by separate brain regions situated in the ATL and AG, respectively, is supported by a confluence of behavioural, computational, neuropsychological, and neuroimaging work (we review some of the neuropsychological and neuroimaging work below). It has also been suggested that the distinct capacities of the ATL and AG may arise out of differences in architecture and connectivity in the brain, i.e. taxonomic relations seem to be *identification*-based, arising broadly out of the ventral *what* stream, while thematic relations seem to be *prediction*-based, arising out of the dorsal *where* stream (Binder & Desai, 2011; Mirman et al., 2017). While we suspect that this suggestion is largely correct, specific neuroanatomically motivated functional networks supporting these relations have yet to be described. Here we begin to fill this gap. To preview, we will propose that the ATL's role in taxonomic processing is supported by connectivity with the perirhinal cortex, which has been shown to aid in *discriminating* between featurally similar objects, and by connectivity with frontal language systems, in particular, the inferior frontal gyrus (IFG), which promotes access to object labels. We also suggest that the AG's role in thematic processing is supported by connectivity with the hippocampal system, which promotes sensitivity to event structure and spatial and temporal co-occurrence.

This paper is organized as follows: We first briefly examine the relative roles of the ATL and AG in taxonomic and thematic conceptual processing. We then turn to our primary proposal: That the semantic capacities of these putative hub regions may arise as a function of connectivity to the perirhinal cortex and hippocampus regions described above. Next, building on work suggesting that there may be a differential role of language (i.e. the label) in processing taxonomic versus thematic relations (e.g. Markman, 1990; Schwartz et al., 2011), we consider several reasons why labelling may be particularly important for taxonomic knowledge. We then propose that neuroanatomical factors (in particular, connectivity with IFG) may help explain why linguistic information supports conceptual processing in the ATL, in particular.

The roles of the anterior temporal lobes and angular gyri in the conceptual system

In this section, we provide a brief review of the involvement of the anterior temporal lobes and angular gyri in the conceptual system, describing some neuropsychological and neuroimaging evidence for their respective roles in processing taxonomic and thematic relations (for a comprehensive review, see Mirman et al., 2017). We also touch on evidence for graded functional differences within the ATL and AG.

Anterior temporal lobe

The anterior temporal lobe has been a major focus of the literature on the neural underpinnings of semantic knowledge. This is largely due to a neurological deficit called *semantic dementia,* an impairment to semantic memory which is caused by degradation of grey matter, as well as underlying white matter, of the ATLs, (for a review, see Hodges & Patterson, 2007). Semantic dementia produces problems with naming, recognizing, and classifying objects regardless of which modality the objects are presented in (e.g. sound, smell, touch, language, and vision; Bozeat, Lambon Ralph, Patterson, Garrard, & Hodges, 2000; Coccia, Bartolini, Luzzi, Provinciali, & Lambon Ralph, 2004; Jefferies & Lambon Ralph, 2006; also see Gainotti, 2011 for a review). With respect to language abilities, semantic dementia manifests in content words being replaced with content-free words such as 'stuff', 'things', and pronominal references (e.g. *her* instead of *my sister Melanie*), and in a prevalence of generalities and high-frequency words (e.g. *stuff* instead of *my collection of souvenir mugs*). In contrast to these semantic deficits, other language and cognitive abilities are relatively intact (Garrard & Hodges, 2000; Hodges, Patterson, Oxbury, & Funnell, 1992; Jefferies & Lambon Ralph, 2015; Snowden, Goulding, & Neary, 1989). Because individuals with semantic dementia tend to be impaired on the same items (i.e. concepts) across a range of semantic tasks and modalities, it has been suggested that the ATL acts as a hub in which general semantic knowledge, i.e. knowledge that is not tied to any individual modality, is represented (e.g. Lambon Ralph & Patterson, 2008; Patterson et al., 2007).

Until recently, most work linking the ATL to semantic processing did not consider whether *sub-regions* of the ATL may vary in terms of their roles in semantic processing. In recent years, however, detailed consideration of the relationship between the anatomical and cognitive progression of semantic dementia has led to hypotheses about specific sub-regions of the ATL supporting different aspects of semantic knowledge. For instance, the hallmark deficit of semantic dementia – difficulty distinguishing among basic-level category members – is associated with damage slightly caudal to the temporal pole, in the anterior inferior temporal lobe and fusiform gyrus (Butler, Brambati, Miller, & Gorno-Tempini, 2009; Mion et al., 2010).

Moreover, as neural degeneration in semantic dementia spreads posteriorly from the temporal pole (for a longitudinal analysis, see Kumfor et al., 2016; see also Brambati et al., 2009; Bright, Moss, Stamatakis, & Tyler, 2008), patients show a characteristic disease-deficit trajectory where deficits in category knowledge progress from loss of specific (e.g. cappuccino) to basic (e.g. coffee) to general knowledge (e.g. beverage; Hodges, Graham, & Patterson, 1995; Rogers & Patterson, 2007). Findings like these have led to the suggestion that the ATL can be characterized as a 'graded' representational hub – i.e., it is the anterior portion of an anterior–posterior gradient along the ventral *what* stream that proceeds from specific to general (see Clarke & Tyler, 2015; Martin & Chao 2001; Mion et al., 2010; for reviews of other suggested sub-regions/gradients within the ATL, see Wong & Galatte, 2012 and Lambon Ralph et al., 2017).[1]

This ventral anterior-posterior gradient from specific (e.g. cappuccino) to general (e.g. beverage) knowledge about the world reflects the way that concepts can be organized hierarchically from subordinate to basic to superordinate – that is, it can be characterized as reflecting taxonomic structure. And indeed, the errors that patients with semantic dementia tend to make can also be characterized as taxonomic errors (e.g. 'cat' instead of *dog*, or 'animal' instead of *dog* can be characterized as category coordinate and superordinate errors, respectively). Importantly, individuals with ATL and/or IFG lesions who do not have semantic

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[1] It has also been suggested that specific category knowledge is lost before general knowledge in semantic dementia because of degree of damage, rather than location of damage (e.g. Rogers et al., 2004). That is, subordinate-level category distinctions are most difficult, and so they are the first to be impaired. As damage becomes more diffuse, progressively easier (i.e. basic and then superordinate) distinctions become more challenging. This pattern holds as long as damage does not affect connections between the amodal hub and specific sensory-perceptual systems. However, this explanation is at odds with neuroimaging evidence that highly similar entities like famous people activate the anterior temporal lobe, while tools activate more posterior parts of the temporal lobe (Damasio et al., 2004; Simmons et al., 2010), and that these same patterns emerge when the respective brain areas are damaged (Damasio et al., 2004). We would not expect this convergence between the imaging and neuropsychological data if the progression from specific to general could be explained entirely by degree of damage.

dementia also show difficulty selecting among taxonomic competitors (Mirman & Graziano, 2012), and there is a strong correlation between ATL lesions and taxonomic errors in picture naming (Schwartz et al., 2009, 2011). Thus, there is good evidence that ATL damage is associated with deficits in processing taxonomic relations.

We suggest that this association may exist, in part, because taxonomically related things, by definition, share features, especially at lower levels of the taxonomy (e.g. *coffee* and *tea* are both dark coloured, warm liquids that have a stimulating effect) and ATL supports *distinguishing* among similar things (e.g. Rogers et al., 2004; Clarke, Taylor & Tyler, 2011). Interestingly, in early semantic dementia, patients have difficulty distinguishing between unique people (e.g. Snowden, Thompson, & Neary, 2004, 2012), and several studies have found that the ATLs are involved in memory for familiar people (for review see Olson, McCoy, Klobusicky, & Ross, 2013). In fact, Olson et al. (2013) have pointed out that specific information often has social or personal significance, and have suggested that the superior ATLs are involved in processing social concepts. On our view, this suggestion is consistent with the gradient proposed above because humans, being relatively similar to each other, can be thought of as highly specific entities (i.e. from a subordinate-level category; see also Patterson et al., 2007) with high featural overlap among category members. As a result, distinguishing between them requires attention to specific details (possibly including their name, i.e. label – we return to the possible importance of the label later).

Neuroimaging work converges with the neuropsychological studies described above. While a large body of neuroimaging work has suggested that the ATL is involved in semantic processing generally (e.g. Binney & Lambon Ralph, 2016; Binney, Embleton, Jefferies, Parker, & Lambon Ralph, 2010; Visser, Jefferies & Lambon Ralph, 2010), often, these studies have used materials targeting taxonomic relations (e.g. rogue–scoundrel; winter–summer; bedroom–kitchen; Binney & Lambon Ralph, 2015; Binney et al., 2010). Moreover, recent work explicitly targeting taxonomic relations indicates that the ATL is particularly active when processing such relationships (Lewis, Poeppel, & Murphy, 2015). Neuroimaging work also implicates the ATL in processing people – the ATL (and temporal pole in particular) is more active for tasks involving people compared to objects such as hammers and buildings (Simmons, Reddish, Bellgowan, & Martin, 2010) or animals and tools (Damasio et al., 2004). In other words, things that can share many features and are therefore difficult to distinguish between (such as people), activate the ATL more than things that are less difficult to distinguish between (tools, buildings, and animals). Thus, like work in neuropsychology, we view the neuroimaging literature on unimpaired individuals as consistent with the idea that the ATL's engagement in taxonomic semantic processing may be due to a role in distinguishing among similar things (for review, see Clarke & Tyler, 2015). Later we consider possible reasons that the ATL plays this role.

Taxonomic knowledge is an important component of semantic knowledge. However, as we pointed out in the introduction, thematic knowledge (the contexts in which things appear) is also an important aspect of semantic knowledge. Yet in many of the studies described above, ATL was less strongly associated with processing thematic than taxonomic knowledge (Jefferies & Lambon Ralph, 2006; Mirman & Graziano, 2012; Schwartz et al., 2009, 2011; Lewis et al., 2015). In the next section, we review work suggesting that another region that has often been implicated in processing semantic knowledge, the angular gyrus, is particularly involved in processing thematic knowledge.

Angular gyrus

In a seminal paper, Geschwind (1972) suggested that the AG acts as a hub for combinatorial processing of word meaning, as it lies at the convergence of visual, auditory, spatial, and somatosensory association areas. In the decades following, a large body of work has confirmed its role in semantic processing. For instance, in a meta-analysis, Binder et al. (2009) assessed the peak activation in semantic contrasts using either spoken or written word stimuli, with AG showing the highest likelihood of activation among all regions in a left-lateralized network. Moreover, AG has been found to be active for words referring to sight, sound, manipulation, and abstract concepts in a lexical decision task (Bonner, Peelle, Cook, & Grossman, 2013), and its activity is correlated with variation on five different sensorimotor attributes (colour, shape, sound, visual motion, manipulation; Fernandino et al., 2015) as well as combinatorial semantic processing across sensorimotor attributes (e.g. *loud car*, *drifting balloon*; Price, Bonner, Peelle, & Grossman, 2015). That is, fMRI studies suggest that during conceptual processing, the AG, like the ATL, processes information from multiple modalities.

Yet unlike the ATL, which seems to specialize in taxonomic knowledge, it has been suggested that AG is particularly critical for processing thematic relations (for a review, see Mirman et al., 2017). Evidence in support of this suggestion comes from both neuropsychological and neuroimaging studies. For instance, voxel-based lesion-symptom mapping has demonstrated that individuals with lesions localized to the left temporoparietal junction (with the highest representation of voxels in AG) are more likely to make thematic errors (e.g. ambulance–fire) in a picture-naming task as compared to patients with ATL lesions (Schwartz et al., 2011). Moreover, individuals with aphasia and lesions to temporoparietal junction show reduced and delayed activation of thematic but not taxonomic relations during word comprehension (Mirman

& Graziano, 2012; for similar findings on object processing, see Kalénine & Buxbaum, 2016; Tsagkaridis, Watson, Jax, & Buxbaum, 2014). Overall, the neuropsychological evidence suggests that thematic deficits appear to arise from damage in the broad locale of the AG, although there may also be functional subdivisions which specialize for object- and language-oriented tasks, as well as subdivisions for semantic and executive processes (in ventral and dorsal AG, respectively).[2]

Neuroimaging studies of unimpaired individuals largely converge with evidence from those with brain damage. The AG is active in processing lexical-semantic thematic relations (Lewis et al., 2015), and the temporoparietal junction is activated by processing thematic relations in objects such as tools and vehicles (Kalénine et al., 2009). Moreover, the AG shows greater sensitivity to two-word phrases that share an event (e.g. "*eats meat*" and "*eats quickly*" share an *eating* event) compared to pairs of two-word phrases that only share a noun that is an argument (e.g. "*eats meat*" and "*with meat*" do not obviously share an event), suggesting that the AG is more sensitive to the information typically denoted by verbs, such as event structure or thematic relations (Boylan, Trueswell, & Thompson-Schill, 2015). That is, the AG might help us to activate the sorts of things that co-occur spatially and temporally with *eating*, or things in our *eating* schema (as in our *morning coffee ritual* schema discussed earlier, where *drinking* might

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[2] Other researchers have suggested a different role for the AG. For instance, Humphreys and colleagues (2015) reported a correlation between task difficulty and AG deactivation (i.e. the more difficult the task, the more deactivated the AG), and suggest that this correlation is compatible with the idea that the AG "acts as a multimodal online buffer of incoming internal or external information" (p. 7861), and that when executively demanding tasks do not require the buffered information, it is inhibited by dorsal parietal cortex (Humphreys & Lambon Ralph, 2015). It has also been suggested that the *ventral* AG supports semantic processing, but the *dorsal* AG is part of a network (which also includes prefrontal cortex) that maintains executive control over semantic processing (Noonan et al., 2013). Consistent with this suggestion, it seems that dorsal AG shows greater connectivity to executive systems in prefrontal cortex (Frey, Campbell, Pike, & Petrides, 2008; Makris et al., 2005), while ventral AG shows greater connectivity to hippocampal regions (Rushworth, Behrens, & Johansen-Berg, 2006; see also Seghier, 2013, Figure 2), which we discuss later as a critical pattern of connectivity in supporting AG's sensitivity to thematic semantic relations.

activate *coffee*, *milk*, *spoon*, and *mug*), consistent with its place in the dorsal *where* stream. In addition to being sensitive to event structure, the AG has also been found to show increased activation when the amount of thematic context in narratives is increased (i.e. comparing discourse versus sentence-level processing of Aesop's fables; Xu et al., 2005), and to be involved when recalling detailed spatial and temporal characteristics from a scene (e.g. recalling details of a video of a train chugging while emitting a loud screech; Bonnici, Richter, Yazar, & Simons, 2016). Taken together, findings like these suggest that the AG may be particularly sensitive to thematic relations by virtue of its involvement in event and scene processing, and sensitivity to the contextual detail therein (Mirman et al., 2017; see also Binder & Desai, 2011).

Hubs shall be known by the company they keep

So far, we have reviewed evidence that the ATL supports processing taxonomic relations, and suggested that this is likely due, in part, to its having a role in distinguishing among similar things. In particular, anterior regions of the ATL appear to be more involved in distinguishing between highly similar/confusable things (e.g. specific-level taxonomic distinctions such as between individual people), whereas more posterior ATL regions distinguish between less confusable things (e.g. general-level taxonomic distinctions; for discussion, see Clarke & Tyler, 2015). We have also reviewed evidence that the AG is generally involved in thematic processing, and suggested that this may be by virtue of sensitivity to contextual characteristics of events and scenes.[3] In the context of these structure-function relationships, we can now turn to our proposal – that connectivity with the hippocampal system may help account for the AG's role in

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[3] In the interest of concision, this was a selective review of research on the neural underpinnings of taxonomic and thematic relations (for a comprehensive review, see Mirman et al., 2017). However, the bulk of work on the issue is consistent with the interpretation put forth above (see, however, Jackson, Pobric, Hoffman, & Lambon Ralph, 2015; Peelen & Caramazza, 2012).

processing thematic relationships, and that connectivity with the perirhinal cortex and IFG may help account for the ATL's role in processing taxonomic relationships; that is, we suggest that their functions can be explained by the company they keep.

Although Damasio's (1989) original convergence zone framework emphasized the importance of more medial and even subcortical structures in higher-level conceptual processing, until recently, much of the literature on hubs has neglected such structures and instead considered the ATL and AG in isolation (but cf. work by Tyler and colleagues; for a review, see Clarke & Tyler, 2015; see also Jackson et al., 2016; Mirman et al., 2017; Lambon Ralph et al., 2017). We speculate that one critical aspect of the different functions of the AG and ATL in conceptual cognition may be the extent to which they are supported by structures lying medial to them, in particular, the hippocampal regions (i.e. the hippocampus and parahippocampal gyrus) and the perirhinal cortex for the AG and ATL, respectively.

Connectivity between AG and the hippocampal system: supporting event structure

Geschwind (1972) observed that the AG is densely connected to modality-specific cortical areas, as well as to the hippocampus, among other distant brain regions such as the IFG and much of the temporal lobe (for review, see Seghier, 2013). Because of this strong interconnectedness, it is fruitful to interpret AG function with reference to this connectivity. We focus here on the AG's connectivity to the hippocampal system, and posterior hippocampus in particular, in part because it is the most proximal system that is densely connected to the AG, and in part because we suggest that it is an ideal candidate for explaining the AG's sensitivity to thematic relations. Earlier, we reviewed evidence that the AG's sensitivity to thematic relations reflects an event-centric role – that is, it is sensitive to temporal and spatial cooccurrence, and accordingly, is activated when we recall the components of an event (as in Bonnici et al., 2016, described earlier), like the concepts at play when we require a warm, stimulating beverage in the morning. Given that the hippocampal system is critically involved in encoding episodic details in space and in time (for a review, see Eichenbaum, 2013), and shows increasing activation with the amount of contextual detail recalled in studies of recollection memory (for a review, see Rugg et al., 2012), we propose that the AG's strong connectivity with posterior hippocampus may account for its sensitivity to the episodic detail and event-based semantics that support thematic relations.

Consistent with this proposal, recent evidence implicates AG in the episodic memory processes we suggest are critical for drawing thematic semantic relations. One account of AG function, called the *context integration hypothesis* (Ramanan, Piguet, & Irish, 2017), holds that the structure of an event (i.e. *what? when? where?*) is coded in the medial temporal lobe (i.e. hippocampal system), while the multimodal details are supported by AG and its dense connections to modality-specific cortical regions. In line with this account, recent empirical work has suggested a causal role of AG in event memory and simulation through the use of transcranial magnetic stimulation (Thakral, Madore, & Schacter, 2017) and continuous theta-burst stimulation (Yazar, Bergström, & Simons, 2017). When given a cue word and instructed to remember or simulate an event related to that cue word, participants show difficulty generating episodic event details following AG stimulation (Thakral et al., 2017). Moreover, after studying visual scenes that were accompanied by an auditory word, participants have more difficulty recalling features following theta-burst stimulation, but only when the task requires multimodal recall (Yazar et al., 2017). Such findings suggest that the AG is critically involved in multimodal simulation of events (see also Bonnici et al., 2016), where the hippocampal system drives sensitivity to event *structure* and AG drives sensitivity to event *content* (Ramanan et al., 2017).

This account of thematic relations is consistent with perspectives on cognition and semantic memory which emphasize simulation in concept processing (e.g. Barsalou, 2009; Bergen, 2012), where processing a concept likely involves accessing thematic relations relevant to that concept.

Connectivity between ATL and perirhinal cortex: discriminability and conceptual structure

With regard to the ATL, we suggest that its involvement in taxonomic conceptual processing may be attributable, in part, to direct connectivity with the perirhinal cortex, which lies medial to it. The perirhinal cortex has feedback connectivity to more posterior regions (Miyashita, Okuno, Tokuyama, Ihara, & Nakajima, 1996), and it may access featural information stored in these more posterior regions in order to facilitate distinguishing amongst entities that are highly confusable, such as taxonomically related entities like animals (which typically have highly correlated features, making it difficult to distinguish amongst them; Kivisaari, Tyler, Monsch, & Taylor, 2012; Wright, Randall, Clarke, & Tyler, 2015; for corresponding evidence in non-human primates, see Saksida, Bussey, Buckmaster, & Murray, 2007). As mentioned earlier, human faces are also highly confusable entities, and so it may be that the ATL's (specifically, the temporal pole's) role in naming famous people (e.g. Damasio et al., 2004; Simmons et al., 2010) is partly attributable to interaction with the perirhinal cortex.

The role of perirhinal cortex (and ATL) in processing feature-based statistics has largely emerged from work on the *conceptual structure hypothesis*, an influential theory of conceptual knowledge inspired by category-specific deficits in semantic knowledge (Tyler, Moss, Durrant-Peatfield, & Levy, 2000; Tyler & Moss, 2001). Category-specific deficits occur when patients show selective deficits in a particular semantic category, such as animals (e.g. Moss et al., 1997) or, less commonly, tools and artefacts (e.g. Hillis & Caramazza, 1991). Under the conceptual structure hypothesis, category deficits specific to animals may arise from lesions to perirhinal cortex: converging evidence between neuroimaging work (Tyler et al., 2013) and lesion-symptom mapping (Wright et al., 2015) suggests that confusability (defined by conceptual structure statistics) and specifically, distinguishing between highly confusable objects or animals, is supported by perirhinal cortex. That is, it is not visually demanding to distinguish between a mug and a spoon because of their low confusability, while distinguishing between a leopard and a cheetah is more challenging. Distinguishing between a cappuccino and a latte requires even more perirhinal support. Importantly, perirhinal cortex appears to be sensitive to both concept-level similarity and visual-perceptual similarity, suggesting that it may promote integration across multiple levels of conceptual structure (Martin, Douglas, Newsome, Man, & Barense, 2018).

Additional evidence that connectivity between the ATL and perirhinal cortex is important for distinguishing among similar things comes from a study using dynamic causal modelling with MEG on patients with left temporal pole and perirhinal lesions, where patients produced fewer category exemplars for some high-similarity categories such as dog breeds and birds, as well as decreased backward connectivity with posterior temporal lobe (Campo et al., 2013). Moreover, disrupting the activity of the left ATL using transcranial theta-burst stimulation leads to impaired performance on recognizing highly similar items presented for a brief period of time, suggesting that anterior temporal regions (lateral and medial) are important for discriminating between highly confusable objects (Chiou & Lambon Ralph, 2016). Thus, feedback relations between ATL and perirhinal cortex, and then with more posterior temporal regions, appear to be critical in discriminating between highly similar entities, an ability that is necessary for representing taxonomic relationships.

Connectivity with the perirhinal cortex may be only part of what supports ATL's involvement in taxonomic processing. Recent work has placed the left ATL within the temporo-sylvian language network (Hurley, Bonakdarpour, Wang, & Mesulam, 2015; see also Bi et al., 2011; Campo et al., 2016; Mesulam et al., 2013). This network includes IFG (which has long been implicated in language function, including semantic control, phonological processing, and syntactic processing; for reviews, see, e.g. Binder et al., 2009; Costafreda et al., 2006; Fiez, 1997) and the middle temporal gyrus. Importantly, strong reciprocal connectivity was found between IFG and ATL via the uncinate fasciculus, suggestive of linguistic mediation of ATL function (Hurley et al., 2015). This connectivity between the ATL and the IFG, in conjunction with the data that we describe in the next section, leads us to propose that the ATL's taxonomic capacity, in addition to being supported by connectivity with perirhinal cortex, may also be promoted by linguistic mediation from the left IFG. Below we expand on how linguistic mediation may help promote taxonomic knowledge.

The role of the label

The idea that language is related in some way to taxonomic category structure is far from new. For example, in her work on child language development, Ellen Markman observed that children given labels show a tendency to sort into taxonomic categories, whereas without labels, they tend to sort thematically (Markman, 1990). From this starting point, we suggest that labels have at least three related functions with regard to processing taxonomic relations: 1) highlighting commonalities among relatively dissimilar members of a category, 2) binding consistent features to create a concept, and 3) adding an additional discriminating feature to highly similar concepts (e.g. people). While the first two functions have been proposed before, the third, as far as we know, has not. In this section we elaborate on these three proposed functions.

First, as others have suggested, labelling may be important for building categories because without a label in common it is challenging to draw commonalities amongst relatively dissimilar members of, for instance, superordinate categories (i.e. labels give us an ‘invitation to form categories’; Waxman & Markow, 1995). For example, having a superordinate label like ‘animal’ allows us to learn, thorough language, that worms and dogs are both are *animals* – that is, we learn their common category membership from their common label. Accordingly, classical views hold that labels are critical for children learning about categories at the superordinate level, and indeed 12- to 13-month-old children show more evidence of having formed categories of objects if the category had been described with a word (Waxman & Markow, 1995). This bias to group objects together if they have the same label means that even concepts which on the surface seem minimally related come to be associated by means of a common label.

Second, and relatedly, labels may help with binding consistent features to create a concept. Lupyan’s (2012) account of *language-augmented cognition* – the notion that using words and language supports cognitive processes such as categorization and memory – suggests that the ATL may be involved in binding the label to the disparate features of a concept, ‘gluing’ them together. For instance, the label might help the smell of coffee, wafting from the kitchen, to evoke gustatory properties of coffee. The idea is that the label is associated with the many features of a concept even when that concept is not present. Because labels are dissociated from particular instances of a concept, they facilitate abstraction over the features most diagnostic of a particular category (Lupyan, 2012). That is, hearing ‘coffee’ is not associated with the gum on the floor last weekend when you stopped at a Dunkin Donuts during a long road trip. Rather, it is associated with the characteristics that consistently occur with coffee (e.g. its smell, taste, and dark colour), as well as things with similar characteristics and that elicit similar experiences to coffee (e.g. tea). Indeed, this property of the label may be one reason that it is particularly useful in the first role we described, i.e., building categories; by facilitating abstraction over the features of a particular category, the label helps highlight commonalities that may not otherwise be obvious.

Finally, we propose that by providing an additional, discriminating feature to highly similar entities, e.g., by adding a person's name to a face, or a model name to a car, labelling is helpful for discriminating amongst them, and thus, for identifying concepts at the more specific/subordinate levels of a taxonomic structure. Thus, the evidence reviewed above that showed that the ATL is associated with discriminating between highly similar entities (e.g. Kivisaari et al., 2012) and naming famous people (e.g. Damasio et al. 2004), may be due not only to ATL's connectivity with perirhinal cortex supporting access to featural information, but also due to ATL's connectivity with left IFG supporting accessing labels. Neuropsychological work further supports the role of ATL in label retrieval – patients with lesions localized to the temporal pole show difficulty with naming unique things, largely without the striking semantic impairments which affect patients with semantic dementia (Bi et al., 2011; Campo et al., 2016; Mesulam et al., 2013). Finally, more direct evidence for this role of the label comes from a transcranial direct current stimulation study which found that that stimulation of the ATL significantly improved naming of famous people (but not naming of famous landmarks, which are not perceptually similar to each other; Ross, McCoy, Wolk, Coslett, & Olson, 2010). This suggests that the label might be a critical feature for our ability to discriminate between, e.g. *cappuccino* and *latte*, two visually similar coffee-related beverages.

Collectively, we suggest that connectivity is fruitful for understanding the ATL's sensitivity to taxonomic relations – medial connectivity to perirhinal cortex supports discrimination among overlapping features, while connectivity to inferior frontal regions supports retrieval of the label. This connectivity to language regions is critical for taxonomic processing because a label may magnify similarities among dissimilar but related categories, help bind together features of a concept, and act as a distinguishing feature of highly similar members of a taxonomy.

A final note on generalization

At the outset, we described ‘generalization’ as the process by which, if a novel object is similar to (i.e. shares attributes with) a known object, then features that are not perceived directly can nonetheless be attributed to the novel object because they can be inferred (i.e. inherited) from the known object’s concept. This kind of generalization is based on taxonomic knowledge – knowledge that determines what kind of thing something is and what it is similar to. But generalization can also be based on thematic knowledge – knowledge about the contexts in which things co-occur (or about the contexts in which one thing predicts that, at a later time, another thing will occur). For instance, I am making a thematic generalization if I assume that my guest would like a spoon and sugar when I pour her coffee – I am generalizing based on my event knowledge for *drinking coffee* to the current situation.

It may appear, therefore, that just as we can distinguish between taxonomic and thematic knowledge, we can distinguish between taxonomic and thematic generalization. However, although for expository purposes we have, so far, described taxonomic and thematic knowledge as distinct, in actuality, we suspect that there is a ‘grey area’ in which knowledge can be both taxonomic and thematic (part–whole relationships like *button* and *blouse* are one example, although there are others, e.g., *spoon* and *mug* are both *tableware*, and they also tend to co-occur). And the same may be true for generalization – there may be cases that are part thematic and part taxonomic (e.g. baristas tend to be observed in the context of brewing coffee, and brewing coffee is also a property of baristas).

We also suspect that just as taxonomic and thematic knowledge are supported by ATL and AG, respectively, taxonomic and thematic generalizations are also supported by these respective regions. Further, we speculate that interactions between these regions may be responsible for the ‘grey areas’. Finally, we imagine that the functions they support, i.e., the statistical abstractions that map individual episodic instances onto accumulated experience, may be similar or perhaps even the same, but that what differs between the regions may be the spatiotemporal resolution over which those abstractions occur. In particular, we speculate that the statistical abstractions supporting taxonomic generalization may be derived over windows of finer spatiotemporal resolution than those that support thematic generalization. However, considerable further research, both empirical and computational, is required before we can understand the relationship, and division of labour between these two regions.

Conclusions

Knowing that coffee is a beverage that is similar to tea (i.e. knowing what kind of thing something is and what it is similar to), and knowing that it is often consumed in the kitchen and stirred with a spoon (i.e. knowing the contexts in which it occurs), are both important components of semantic knowledge. In this review, we have briefly summarized evidence that these two types of semantic knowledge, which – in keeping with the literature – we have described as taxonomic and thematic, respectively, rely differentially on two different brain regions: the anterior temporal lobe and the angular gyrus (for a comprehensive review, see Mirman et al., 2017). We then put forth a proposal about why these two regions may be particularly well-suited to supporting taxonomic and thematic relations, respectively.

Specifically, we have suggested that the angular gyrus may be particularly well-suited to supporting thematic knowledge because of this region's strong reciprocal connectivity with, and close proximity to, posterior hippocampus. This connectivity supports this region's capacity to be sensitive to spatial and temporal episodic detail, and accordingly, event structure, from which thematic relations are generalized. We have also considered two reasons that the anterior temporal lobe may be particularly well-suited to supporting taxonomic knowledge. First, connectivity with perirhinal cortex may support discerning and discriminating between featurally similar objects, and second, connectivity with the prefrontal cortex may allow the latter region to support selecting the appropriate label for objects, which tends to highlight taxonomic relations. In sum, we suggest that the way that the angular gyrus and the anterior temporal lobe (which have typically been considered general semantic regions) interact with medial cortical and even subcortical structures may help explain their apparently different roles in supporting generalized feature-based (i.e. taxonomic) and event-based (i.e. thematic) knowledge.

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