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Graded specialization within and between the anterior temporal lobes

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Considerable evidence from different methodologies has identified the anterior temporal lobes (ATLs) as key regions for the representation of semantic knowledge. Research interest is now shifting to investigate the roles of different ATL subregions in semantic representation, with particular emphasis on the functions of the left versus right ATLs. In this review, we provide evidence for graded specializations both between and within the ATLs. We argue (1) that multimodal, pan-category semantic representations are supported jointly by both left and right ATLs, yet (2) that the ATLs are not homogeneous in their function. Instead, subtle functional gradations both between and within the ATLs emerge as a consequence of differential connectivity with primary sensory/motor/limbic regions. This graded specialization account of semantic representation provides a compromise between theories that posit no differences between the functions of the left and right ATLs and those that posit that the left and right ATLs are entirely segregated in function. Evidence for this graded account comes from converging sources, and its benefits have been exemplified in formal computational models. We propose that this graded principle is not only a defining feature of the ATLs but is also a more general neurocomputational principle found throughout the temporal lobes.

Keywords: anterior temporal lobes; conceptual knowledge; semantic memory; laterality; hemispheric specialization

Introduction

Over the past 20 years, considerable convergent evidence from different methodologies has highlighted a critical role for the anterior temporal lobes (ATLs) in multimodal semantic representation across a wide range of concept types, including concrete, abstract, emotion, and social meanings.[1–10] Research interest has now shifted, at least in part, to the role of different subregions of the ATLs in representing semantic knowledge. This includes a specific interest in the roles of the left versus right ATLs in conceptual processing, with differential predictions being made in the current literature. Some researchers propose that left and right ATLs operate as a single, integrated system,[1,5,11–13] whereas others have offered alternative, varying hypotheses, each of which propose distinct roles for the left and right ATLs.[7,14–18] In the current review, we provide evidence for graded organization of function within and between the left and right ATLs, showing that transmodal, pan-category semantic representations are shared across the left and right ATLs. We further suggest that this graded principle is not only a defining feature of the ATLs but is also a more general neurocomputational principle found throughout the whole temporal lobe (for a related account of left versus right ventral occipitotemporal (vOT) functions, see Ref. 19).

Role of the bilateral versus unilateral ATLs in conceptual knowledge

Our consideration of this topic begins with the more general hypothesis that conceptual representations are formed and activated by an ATL "hub-and-spoke" framework[5,20] (Fig. 1A). As per classical models of conceptualization, verbal and nonverbal

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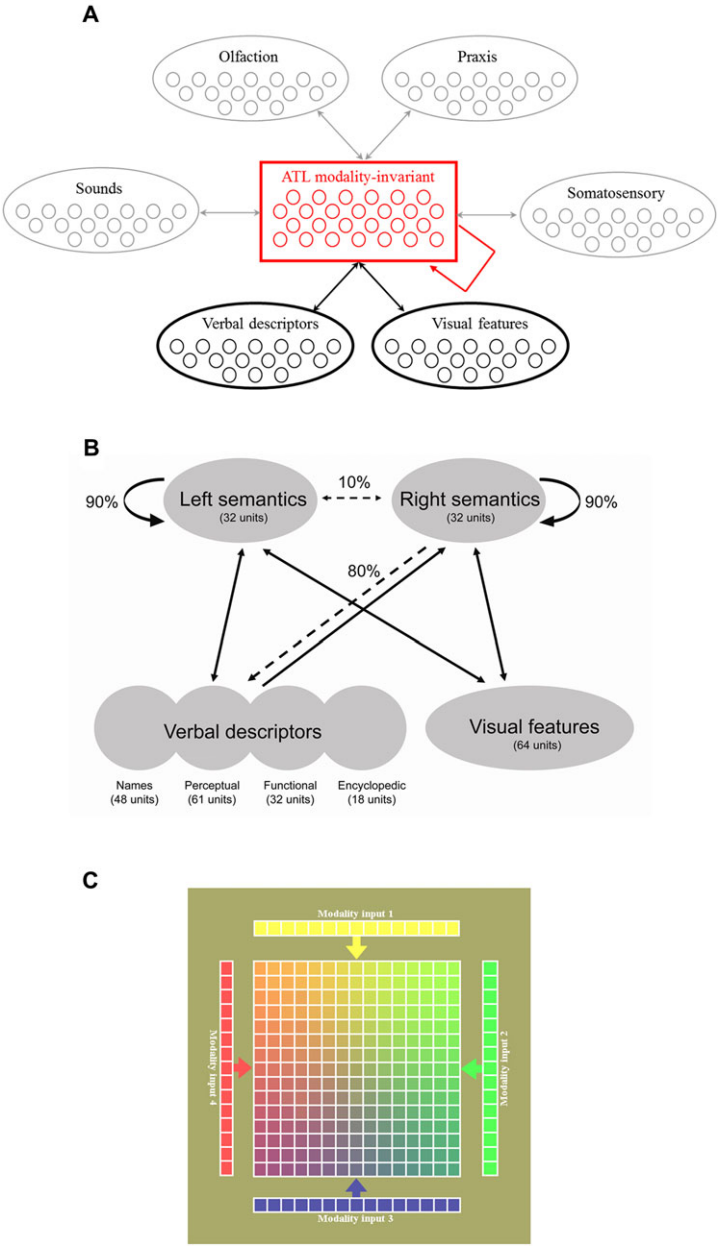

Figure 1. The evolution of the hub-and-spoke model of semantic representation. (A) The hub-and-spoke model as implemented by Rogers *et al.*[20] Generalizable and coherent semantic representations are formed from the interaction of modality-specific information through a transmodal representational "hub" layer. Accordingly, semantic representations reflect the joint action of both hub and spokes (see text). (B) The demi-hub-and-spoke model as implemented by Schapiro *et al.*[12] The core characteristics of this model are the same as the standard hub-and-spoke computational framework with the exception that the hub layer is split into two "demi-hubs" with high levels of connectivity from each left and right hemisphere demi-hub to the modality-specific spoke regions. The two demi-hubs are interconnected at a lower probability. Despite lower levels of connectivity than the original hub-and-spoke model, the demi-hub model is able to form coherent semantic representations that are relatively robust to unilateral damage (see text for details). (C) The graded hub-and-spoke model (see Refs. 11, 23, 41, and 85). Again, this model is very similar in form to the standard hub-and-spoke model with the exception that the relative strength of connections from each hub unit is governed in part by its distance to the modality-specific source of information. The result is that the entire representational hub layer is still implicated in semantic representation, but the relative contribution of each unit is graded across the hub (see text).

sensory experience gives rise to distributed activation patterns across the primary association cortices, and modality-specific representations/engrams (reflecting the statistical structure in each of these domains) are supported by the corresponding secondary modality–specific association regions. Each of these "spoke" regions interacts with the transmodal ATL "hub," whose function is to distil coherent concepts from our multimodal verbal and nonverbal experience, and thus generalize and discriminate appropriately across semantic exemplars.[1,2,20] Accordingly, semantic representations reflect the joint action of the transmodal ATL "hub" and the various unimodal "spoke" regions.

Anatomically, the ATLs are well placed as information-convergence zones within the brain.[21–23] In humans and primates, the ATL region is strongly connected to a variety of cortical regions, including primary sensory cortices, posterior temporal and occipital cortex, medial structures (limbic cortices, hippocampal systems, and olfactory systems), and frontal systems that play roles in executive function and social cognition/valence.[21,23–26] The pattern of long-range, major white matter tracts also emphasizes the hub-like connectivity of the ATL region,[27,28] including convergence of the inferior longitudinal fasiculus (from posterior vOT and occipital areas), the middle longitudinal fasciculus (from inferior parietal and primary auditory regions), the uncinate fasciculus, and perhaps branches of the inferior frontal–occipital fasciculus (from various orbitofrontal, lateral frontal, and limbic regions).

Contemporary interest in the ATLs as a key conceptual region has primarily stemmed from studies of patients with semantic dementia (SD) who have a selective yet progressive transmodal, pan-category semantic impairment of conceptual knowledge.[29–31] Although SD patients suffer from cortical atrophy throughout the ATL region, bilaterally, the ventrolateral surface of the ATLs is the area of maximal atrophy, and damage to this part is most strongly correlated with semantic performance in these patients.[32,33] The same ventrolateral region has also been directly implicated in conceptual knowledge via direct intracortical recordings and stimulation.[9] Although this region has not been prominent in the functional magnetic resonance imaging (fMRI) literature, this seems to reflect a set of methodological issues, including reduced field of view, the nature of the baseline task, and magnetic inhomogeneities in this and other susceptible regions.[4,34] Recent methodological advances have reduced these problems,[35–37] and the resultant fMRI studies have observed strong ventrolateral activation in the left and right ATLs across a range of verbal and nonverbal semantic tasks.[38–43] These activation peaks also overlap with positron emission tomography and magnetoencephalography imaging studies of semantic tasks,[6,44] further supporting the hub-and-spoke notion that the ATL region, left and right, acts as an integrative store of transmodal, pan-category conceptual knowledge.

In the first computational instantiation of the hub-and-spoke hypothesis[20] (Fig. 1A), the ATL hub was implemented as a homogeneous, single functional processing layer (which might arise from a single neural region or multiple, heavily interconnected areas). As we shall go on to discuss, both of these features (homogeneity and unitary) have been revised in subsequent models, as our focus has broadened to consider the relationship between left and right ATLs. The "demi–hub and spoke" model of semantic representation proposes that the left and right ATLs work in tandem as a bilateral, interactive, partially redundant semantic system[1,5,11,12,45,46] (Fig. 1B). This bilateral representational hypothesis arises from consideration of SD patients, as their profound semantic deficits are always associated with bilateral atrophy,[29,47] albeit often asymmetric: in most cases during the early stages of the disease, atrophy is asymmetric, with one hemisphere relatively more atrophied compared to the other.[29,48]

In contrast to the substantial semantic impairments observed in SD patients, recent studies exploring semantic function in patients with unilateral ATL resection (to either the left or right ATL) because of intractable epilepsy or removal of glioma have shown much milder semantic deficits.[45,49] Although mild expressive and receptive semantic deficits can be observed in patients with temporal lobe epilepsy, these are only apparent in the most demanding and therefore sensitive assessments.[46,50] This suggests that semantic performance is much better preserved in patients with unilateral ATL damage than it is after bilateral ATL damage (a difference that may be exacerbated by the different types of acute versus progressive etiology of each patient group[12,51]). Intriguingly,

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these contemporary patient data mirror the older and well-known comparative neurological work in primates, who after bilateral ATL resection showed a chronic and substantial semantic impairment as part of a wider Klüver–Bucy syndrome (unilateral resection, in contrast, elicited a milder yet transient impairment[52–54]). Although these studies are most often cited for the primates' behavioral deficits and visual agnosia caused by the bilateral resections, both Klüver and Bucy, and Brown and Schafer noted that each primate exhibited clear evidence of multimodal, trans-category semantic deficits ("He gives evidence of hearing, seeing, and of the possession of his senses generally, but it is clear that he no longer clearly understands the meaning of sounds, sights, and other impressions that reach him . . . . This is the case not only with inanimate objects, but also with persons and with his fellow Monkeys" (Ref. 52, pp. 310–311)). This same pattern has been replicated in a rare human case study, again showing that, after preliminary unilateral ATL resection (due to persistent intractable epilepsy), semantic deficits were relatively mild, but after removal of the contralateral ATL, severe semantic impairments were evident.[55] Similar organizational principles have also been found in the episodic memory literature, where unilateral removal of the hippocampus results in mild memory impairments, whereas simultaneous bilateral removal of the hippocampi gives rise to gross anterograde amnesia.[56]

This key observation that, in contrast to bilateral lesions, unilateral damage produces relatively little behavioral disruption has been replicated and explored in a computational model by Schapiro *et al.*[12] In an extension of the Rogers *et al.*[20] hub-and-spoke computational model, the transmodal representational hub layer in the model was divided into left and right "demi-hubs" (representing the left and right ATLs (Fig. 1B)). When one demi-hub was damaged, the model's performance was only mildly compromised; when both demi-hubs were damaged, however, the model's semantic performance became severely impaired. Critically, this result held even when the total amount of damage was equated across the unilateral versus bilateral lesions, and it became more pronounced after a period of spontaneous recovery.[12] Although the Schapiro model is primarily a bilateral, interactive model of semantic representation, importantly, it does not preclude graded specialization in each demi-hub, and we shall explore the evidence for such specialization over the course of this review.

The Schapiro model deals specifically with the divergent effects of unilateral and bilateral ATL damage. However, the importance of both left and right ATL regions (particularly in ventrolateral areas[42]) in semantic processing can also be found in neurologically intact participants. For example, when using functional neuroimaging techniques that either avoid or correct for technical challenges associated with imaging this region (see Ref. 4), the same bilateral ATL involvement is found across a range of verbal and nonverbal semantic tasks.[6,40–42,57] Similarly, stimulation to either the left or right ATL using repetitive transcranial magnetic stimulation (rTMS) results in equivalent levels of transient yet selective semantic impairment.[3,58] This outcome is shown multimodally, across both verbal and nonverbal semantic tasks,[13] and is selective to the ATLs, as stimulation to "control" areas outside the ATL does not produce the same response.[59] Finally, the importance of the interaction between the left and right ATL hub regions has been highlighted by a recent study that combined rTMS and fMRI.[60] This investigation found that, following left ATL stimulation, in addition to the expected inhibition of activity under the stimulation site, there was also upregulation of activity in the right ATL. Thus, just as the effects of left unilateral ATL resection are partially ameliorated by the contribution of the intact right ATL, so transient disruption to left ATL function results in a compensatory increase in activity in the contralateral ATL. These online changes in the contribution of the two ATLs not only underline the apparent bilateral characteristics of the normal semantic system but also offer potentially important insights about recovery of function following permanent damage (as observed in patients with unilateral lesions).

Differences in left versus right ATL function

So far, we have outlined a model of ATL function in which semantic knowledge is supported by interactive, bilateral activation across the ATLs. In this section, we discuss evidence for differences in the functions of the two ATLs, before considering how a primarily bilateral model might account for these distinctions. A number of researchers have proposed differences between left and right ATL function on

the basis of (1) the modality of the stimulus being processed,[14] (2) the nature of the semantic task being performed (speech production versus visual recognition/receptive processing),[16,61] and (3) the social content of the stimulus.[62,63] Evidence for these standpoints primarily comes from the comparison of patients with left ATL atrophy/resection versus those with right ATL atrophy/resection.

Modulation of ATL function based on input modality

The input modality account[14,15,64] predicts differences in left versus right ATL function based on the modality of the stimulus, with the left ATL associated with processing verbal inputs (written and spoken words) and the right ATL linked with nonverbal information.[30,65,66] Evidence from this standpoint originates from studies of SD patients with bilateral yet asymmetric damage. Snowden *et al.*[30] directly compared the performance of SD patients with left > right or right > left ATL damage on famous face versus written name recognition tasks. Performance on both tasks was impaired in the left > right and right > left patient groups, compared to an older adult control group, and the patients demonstrated significant levels of item association across the two versions of the task (i.e., the status of an item on the verbal version of the task predicted the patients' performance on the nonverbal, and vice versa). Both these outcomes are classically considered to be evidence of damage to a unitary semantic system. In addition, second-order group differences also emerged. Left > right patients performed somewhat more poorly on the written name recognition task relative to the right > left group; whereas, right > left patients' performance on the face recognition task was weaker than the left > right group. Similar conclusions (i.e., bilateral representation with second-order differences across hemispheres) have been drawn from investigations that have explored the relationship between semantic performance and the integrity of ATL gray matter. Butler *et al.*[33] studied patients with progressive language deficits of mixed etiologies and correlated their performance on word and picture versions of semantic tasks with their degree of damage in each voxel. Damage to both ATLs was negatively correlated with performance on both semantic tasks. In addition, damage to the left ATL was more strongly correlated with performance on the word-based version and right ATL damage with performance on the picture-based version.

Modulation of ATL function based on word retrieval

Similar to the input modality hypothesis, the word retrieval/visual recognition account[16,17,61] makes predictions about ATL laterality based on whether a semantically driven spoken response is required versus access to semantic knowledge from visual input (e.g., face recognition). Accordingly, the left ATL is associated with word retrieval tasks (e.g., picture naming) and the right ATL is associated with other tasks (e.g., visual recognition). Again, this account is based on the comparison of patients with left versus right ATL damage.[16,17,67] For example, Acres *et al.*[67] correlated patients' performance on naming and object recognition with voxel-based morphometry measures of temporal lobe integrity. Damage to the left ATL was correlated with scores on naming tasks and damage to the right ATL was correlated with scores on visual recognition tasks. The left ATL effect for naming has been repeatedly replicated across diverse etiologies such that patients with either unilateral left or left > right bilateral damage exhibit a greater anomia than patients with right-sided lesions.[17,45,46,48] According to the Damasio–Tranel account, the left ATL is responsible for the process of lexical access from semantic knowledge, whereas the right ATL is specialized for visual recognition.[16,17,68]

Modulation of ATL function based on social processing

The third account of differential ATL function suggests that laterality differences between the hemispheres reflect the social content of the stimulus.[7,62,63] On this account, the right ATL is considered to be relatively specialized for processing social concepts, consistent with long-standing observations that the ATLs are involved in social cognition in humans and primates.[54,69–72] More recently, several groups have proposed that all or part of the ATLs selectively code social concepts, including person knowledge and emotional concepts.[62,63,72–74] Indeed, deficits in social behavior are often observed in SD patients, including social awkwardness, person-recognition deficits, and a loss of empathy.[75,76] This could either reflect a dedicated role of ATL regions in social concepts and/or the contribution that a more generalized ATL semantic system might play in activation of social concepts.

With regard to the involvement of left versus right ATLs in social conceptual processing, the results in the current literature are very inconsistent. Clinically, it has been argued that the social impairments in SD patients are typically more severe, or more obvious, when atrophy is right > left.[69,74–77] In a novel extension from these clinical findings to fMRI, Zahn *et al.*[72] demonstrated that activation associated with socially related words (e.g., polite) versus nonsocial words (e.g., nutritious) was localized to the right anterior superior temporal gyrus (STG) in neurologically intact participants. However, a more recent direct replication of the Zahn *et al.* task found greater left than right ATL activation,[63] suggesting that both ATLs may play a role in this task. Indeed, the potential role of the left as well as right ATL in social concepts was underlined by the study of Chan *et al.*,[76] which, in a formal exploration, found social and behavioral deficits in both left > right and right > left SD patients (with a greater proportion of right > left, albeit more severe, SD patients showing social and behavioral deficits).

Potentially related to the social ATL hypothesis, laterality effects have been reported for processing people's names and familiar faces, with the left ATL associated with processing names and the right ATL with familiar faces.[17,30,65,66,78,79] This forms part of a more general, ongoing debate as to whether the ATLs preferentially process person knowledge versus other conceptual categories[73,78,80] or whether the ATLs represent information from different conceptual categories with equal weightings. In keeping with the social ATL hypothesis, these accounts note that the ATL regions might be preferentially involved in representing knowledge about people as a part of a more general role in coding social information. The alternative hypothesis is that the ATL regions have a more general semantic representational role, in keeping with the fact that activation in neurologically intact participants and deficits in SD patients are observed across a wide range of categories with no particular social relevance.[38,39,81,82] According to this perspective, the relatively prominent ATL activation/impairments for person knowledge reflect the fact that this is a densely populated area of semantic knowledge, in which specific individuals must be distinguished from one another despite having highly overlapping visual and semantic properties. This individuation of entities at a highly specific level places intrinsically greater demands on the semantic system.[1,20,83]

Relative modulation of ATL function in neurologically intact participants

The three accounts outlined above all predict differences in the functions of left versus right ATL, based primarily on the comparison of patients with left versus right ATL damage. On the face of it, these data pose a challenge to our assertion that the ATL semantic system is bilateral in its organization. However, it is important to note that the differences between the left and right patient groups are invariably relative rather than absolute. Taking the most robust behavioral difference as an example, left ATL patients nearly always have greater anomia than right ATL patients; however, patients with right-dominant ATL damage also show a degree of naming difficulties.[17,46,48] This suggests that the conclusions drawn from patient studies may have been overstated and that the reality may be less modular/unilateral in nature than some have suggested.

Given the previous heavy reliance on patient data alone, a recent large-scale meta-analysis of the functional neuroimaging literature in neurologically intact participants considered the predictions of all three unilateral accounts (input modality, word retrieval, and social concepts) simultaneously.[11] The results supported the hypothesis of a bilateral ATL system underpinning normal semantic processing by showing, first and foremost, bilateral activation across a range of tasks.[11] Secondary hemispheric differences (relatively stronger activation in the left hemisphere) were also shown when participants were asked to name a stimulus or when they were asked to read a written word. In contrast, no right-lateralized response to nonverbal pictorial tasks or social concepts was found.[11] Critically, even when hemispheric asymmetries were found, they were in the context of (1) an overall bilateral involvement in semantic processing and (2) as we shall come to in the next section, more robust functional differentiation within each ATL than across hemispheres (a pattern also found in a previous meta-analysis of the literature[4]). These results mirror those found in neuropsychological studies, namely that most semantic tasks are supported by the ATLs bilaterally, with the exception of a relatively increased reliance on the left ATL during verbal

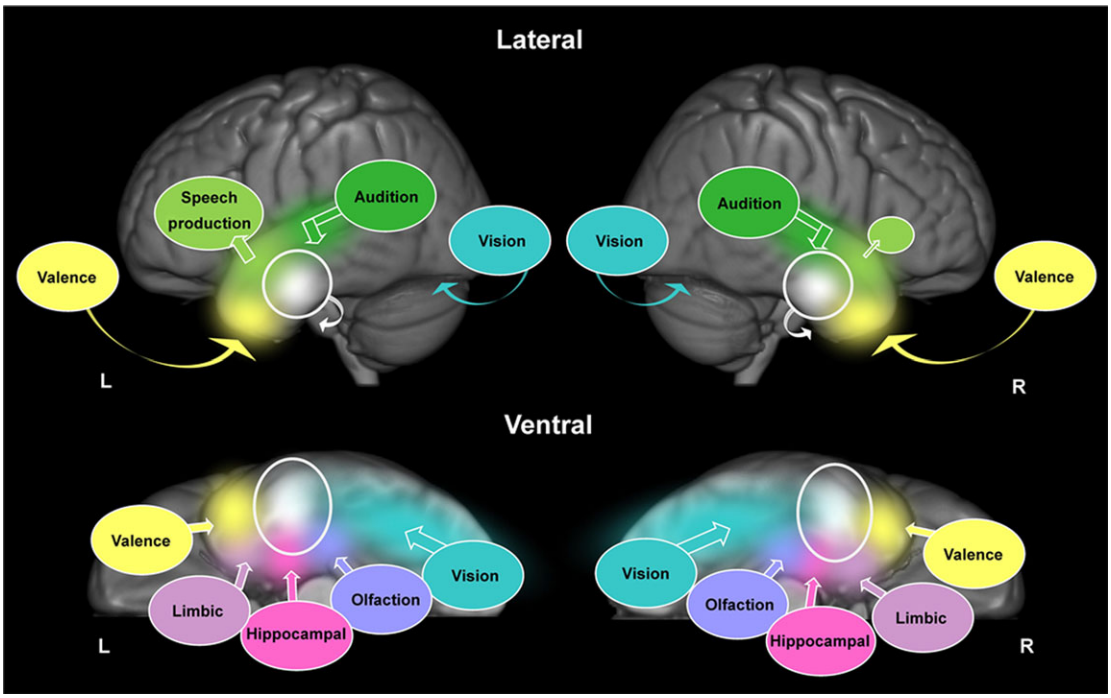

Figure 2. Illustration of the bilateral yet graded representation of conceptual knowledge across both ATLs.[11] The ventrolateral portions of the ATLs, bilaterally (white circles), receive converging inputs from the primary sensory cortices and medial temporal structures (colored circles). The different colors represent information from these different input regions converging upon the ventrolateral ATLs, eventually becoming mixed (white). Bold arrows illustrate the direction of convergence. Curved arrows illustrate the direction of activation that cannot be seen on the lateral surface; for example, visual information travels along the ventral surface of the temporal lobes via the fusiform gyrus. Differential connectivity is illustrated as speech output regions in the frontal lobes are larger in the left hemisphere compared to the right hemisphere (light green circles).

production and written-word processing. Indeed, during tasks requiring orthographic processing in neurologically intact participants, the right ATL has been shown to be deactivated compared to rest.[84]

The graded hub-and-spoke account of conceptual knowledge

We began this review by presenting evidence that both ATLs function together as part of an integrated semantic system. We have also seen that neuropsychological and functional neuroimaging literatures indicate subtle but important differences between left and right ATLs, though these are graded rather than absolute in nature. To account for all of these findings, we have developed a bilateral, graded hub-and-spoke model (Figs. 1C and 2). This neurocomputational framework for ATL function is guided by information about the structural and functional connectivity of the ATL region. It incorporates an overall bilateral representation of semantic knowledge (cf. Ref. 12), but also allows for some graded functional specialization, emerging as a result of differential and asymmetric connectivity (Fig. 1C; cf. Ref. 85) between ATL subregions and various primary sensory–motor and limbic regions.[1,11,23,41,42] As described earlier, the ATLs are directly connected to a variety of cortical regions via major fiber bundles, and this system of diverse inputs and outputs makes this region ideally suited for developing transmodal conceptual representations. We propose that variations in the strength of these connections across the two ATLs, and within each ATL, lead to graded specializations in the types of information in different parts of this system. On this account, the ATLs as a whole act as a representational hub, and second-order specializations emerge based on the differences in the specific inputs and outputs received by different parts of this system.

Recent fMRI in healthy subjects,[38–40,42,43] cortical electrode implantation,[9] and damage-deficit correlations[32,33] have converged on the ventrolateral ATLs as the epicenter of the pan-modal, pan-category semantic system. We propose that this region forms the center point of a graded representational space. According to the graded hub-and-spoke theory, movement away from the ventrolateral ATL "center point" results in graded changes in functional specialization (colored areas in Fig. 2), reflecting the proximity/connection strength to modality-specific sensory, motor, or limbic regions. Accordingly, the closer an ATL subregion is to an area of specialized cortex, the more specialized its graded function will be (for a computational implementation of this idea, see Ref. 85). One example of this is the ventral/dorsal distinction for visual/auditory inputs.[4,11,41,42,86] In contrast to the multimodal activation observed in the ventral ATL core region, visual inputs differentially activate more posterior ventral temporal areas (light blue in Fig. 2), whereas auditory stimuli activate dorsal parts of the ATL (anterior STG (green in Fig. 2)). Of course, this functional differentiation mirrors the positioning of the primary sensory regions, with the primary visual cortex in the occipital cortex and the primary auditory cortex located in Heschl's gyrus.

Additionally, following the same connectivity–function principle, we hypothesize that graded hemispheric differences between the left and right ATLs arise from two potentially linked sources: (1) hemispheric asymmetries in the structural white matter pathways and (2) asymmetries in the functional connections between the ATLs and higher-order cortex.[11,48,87] The rapid increase in tractography data over the past 10 years has shown that the physical, structural connections of the brain are generally bilateral and symmetrical.[88,89] The one exception is that segments of the arcuate fasciculus have been shown to be more robust in the left hemisphere.[90,91] It is also well established that the language network is lateralized in the left hemisphere, both for spoken word production in the prefrontal cortex[92] and for orthographic processing in the left vOT cortex.[93–95] Thus, these (potentially linked) sources of asymmetric functional and/or structural connectivity may well underpin the increased reliance on the left ATL region for naming and written-word recognition. Indeed, stronger connections between the left ATL and left-lateralized speech output system are a feature of both the Schapiro computational model and an earlier computational model of SD.[12,48] In the Schapiro model,[12] the left demi-hub was more strongly connected to speech output representations than the right, with the consequence that damage to the left (in comparison to the right) demi-hub produced more substantial anomia despite equivalent levels of semantic impairment overall. This mirrors repeated observations of greater word finding difficulties in patients with left > right ATL damage in neurodegenerative diseases or left versus right ATL resection.[17,45,46,48,96]

We should note here that one other potential structural asymmetry has been proposed to underpin the right hemisphere prevalence for social concepts.[63,97] Postmortem studies of healthy participants and patients with schizophrenia have shown stronger connectivity, via the uncinate fasiculus, between the right ATL and orbitofrontal regions involved in social and emotion processing.[97] However, more recent diffusion tensor imaging work has provided contradictory findings.[62,98,99] Thus, both the dependence of social concepts on left versus right ATL and the white matter asymmetries that might underpin this are currently unclear and require further careful anatomical and functional investigation.

The posterior temporal lobes are another region in which asymmetric functional connectivity within the left and right hemispheres has been consistently reported (see Ref. 19 for a more in-depth discussion). These connectivity differences might explain why the left vOT cortex becomes relatively specialized for orthographic processing[87,95] and the right vOT cortex for face processing.[100] These specializations in the occipitotemporal cortex may also have functional consequences for the ATLs. If the effect of this functional asymmetry is propagated rostrally along the temporal lobes, then, necessarily, the left ATL will receive more orthographic input than the right ATL and, conversely, the right ATL will receive more face processing input compared to the left. As noted above, this differential functional connectivity could explain the left-lateralized pattern of activation observed for written word tasks in the Rice *et al.*[11] meta-analysis. In addition, the same notion could explain the apparent right-lateralized face recognition/comprehension

impairments noted in the neuropsychological literature. Indeed, this link between the right posterior temporal lobes (in the "core" face processing network) and the right ATL (in the "extended" face processing network) has been shown to be critical for normal face processing.[101] Patients with congenital prosopagnosia (who have deficits in face recognition without a discernible cortical lesion) do not show activation in the right ATL during face recognition tasks compared to healthy controls but do activate the fusiform face area normally.[101] Consistent with the connection–function principle set out above, it has been argued that these results from congenital prosopagnosia reflect a disconnection disorder between the posterior and anterior temporal lobes. In support of this hypothesis, patients with congenital prosopagnosia have reduced gray matter volume in the anterior fusiform gyrus, which correlates with their performance on face-processing tasks.[102] A similar disconnection between posterior and anterior face-processing areas has recently been proposed to underlie face-processing deficits in temporal lobe epilepsy.[103] Indeed, these temporal lobe epilepsy patients were found to have reduced integrity of the inferior longitudinal fasciculus ipsilateral to the side of resection and reduced activation in the occipital face areas.[103]

In concluding this subsection, we note two additional points. First, despite some evidence for a right-lateralized temporal face network, there is an ongoing debate in the literature regarding whether the right ATL is specialized for face recognition per se or whether its responsiveness to face stimuli is a consequence of coding more general, transmodal, person knowledge.[104–106] Although activation of the right ATL for face stimuli has often been taken to indicate a specific face-recognition function for this region, few studies in this face-specific literature have simultaneously probed face versus non-face concepts in the ATL region. This leaves open the possibility that the right ATL contribution to face and person knowledge is just one aspect of the more general ATL semantic system we argue for in this article. Second, despite these asymmetries in functional connectivity (for speech, written word processing, and face recognition), in the context of semantic processing more generally, there is always a degree of bilateral ATL activation, and the left–right differences are graded and relatively subtle in nature. Indeed, it would appear that the hemispheric asymmetries are stronger outside of the ATL regions (e.g., in the posterior temporal cortex and the frontal cortex) than within them.[11] This pattern suggests that the ATLs themselves are not strongly segregated in function (consistent with the convergent nature of their connections, which should, by definition, drive function to become more homogenous) and that the graded hemispheric differences reflect the subtle variations in function/structural connectivity.

Why is a bilateral yet graded system useful?

We have described a bilateral yet graded model of semantic cognition whereby both ATLs play critical roles in normal semantic processing, with graded specializations emerging from differential connectivity to other temporal and extratemporal regions. The principal advantage of having a bilateral system is that it is more resistant to damage. On this view, the left and right ATLs can be thought of as a functionally unitary semantic system. As a result, unilateral ATL damage can be compensated/recovered (at least partially) by the remaining ATL, whereas bilateral damage diminishes the possibility of recovery.[45,46,49] Indeed, as reviewed above, both human and primate investigations have shown that performance is better preserved after unilateral than bilateral damage.[45,54,55]

We have already noted that Schapiro *et al.*'s[12] bilateral model of ATL function, which used a demi-hub-and-spoke architecture, demonstrated disproportionately mild deficits when exposed to unilateral relative to bilateral damage. Formal mathematical analysis was able to explore the basis of this robustness to damage.[12] The model was based upon the unitary hub-and-spoke Rogers model[20] and was identical in all regards except that the hub was split into two separate pools of processing units, analogous to each ATL (Fig. 1B). The resultant demi-hub model was still able to learn the training set and generate semantic-like representations. In addition, mirroring the empirical data, it demonstrated greater semantic impairment after bilateral than unilateral damage, even when the total amount of damage was held constant. Formal analyses of the model demonstrated that this effect reflected and was modulated by three factors. First, following unilateral damage, the undamaged demi-hub still generated clear semantic structure across its internal representations sufficient to

maintain an accurate response (albeit probably activated more slowly than in the case of an intact bilateral system). Second, even small amounts of postdamage recovery magnified the difference between unilateral and bilateral damage.

Finally, detailed analyses of the model demonstrated that there was an important interaction between the model's architecture and the nature of damage. Within each demi-hub of the model, all of the processing units were fully connected to one another. However, the two demi-hubs were only sparsely connected with one another (mimicking the bias in the brain toward short-range, intrahemispheric connections[107,108]). In this type of model, where representations are coded in a distributed manner across a set of weighted connections, damage not only weakens the strength of the representation but also adds noise to the remaining information, which can be propagated to highly connected parts of the network. Consequently, when damage is restricted to one demi-hub, its representations are weakened and distorted, but, because of the limited connectivity between the two demi-hubs, the effect of this distorted signal is relatively isolated. In comparison, when damage is bilateral, the noise within the left and right demi-hubs distorts all aspects of the remaining semantic information.[12]

One intriguing potential implication of distributed cognitive functions across bilateral brain regions is that the brain areas that support recovery of function in patients after unilateral damage are the same brain regions that are recruited during challenging processing conditions in the healthy system. In other words, recovery can involve re-optimization of existing resources, whereby contralateral regions that were already somewhat involved in supporting the affected functions simply upregulate their contribution to compensate for the damage. Evidence for this type of compensation/upregulation in the contralateral hemisphere has been found in the language/semantic domain after stroke[109,110] and for long-term recovery of episodic memory function after resection for temporal lobe epilepsy.[103,111,112] In neurologically intact participants, this same mechanism has been demonstrated for semantic aspects of language.[44] A combined fMRI–TMS study in the motor domain has gone beyond this idea to show that the upregulation in the contralateral hemisphere is functionally relevant.[113] O'Shea *et al.*[113] showed that, after 1-Hz rTMS to the left dorsal premotor cortex, activation in the right hemisphere homologue increased as a compensatory mechanism. The researchers then explored whether this upregulation was functionally relevant by applying additional stimulation to the right dorsal premotor cortex (following the left premotor stimulation). The results showed that performance on an action–selection task decreased following the second round of stimulation to the right premotor cortex.[113] Direct evidence for interhemispheric compensation between the ATLs comes from a recent combined fMRI–TMS study in neurologically intact participants. Binney and Lambon Ralph[60] applied 1-Hz offline rTMS stimulation to the left ATL before participants were placed in the MRI scanner. Results showed that, as expected, there was reduced activation under the site of stimulation but that there was task-specific upregulation of activity in the right ATL homologue. This result suggests that, following rTMS-induced disruption to the left ATL, the healthy semantic system simply upregulates the existing resources that are already involved in the task in order to compensate for the disruption and maintain normal semantic processing. This upregulation of the contralateral hemisphere may be responsible for maintaining semantic processing in patients with unilateral resection; although, given the current paucity of neuroimaging evidence comparing pre- versus postsurgery reorganization, this hypothesis remains untested.

Importantly, as well as providing a potential explanation of the differential effects of unilateral versus bilateral damage and of recovery following damage, the bilateral hub-and-spoke account also extends the effects of connectivity differences to variable functional recovery. Thus, for example, although semantic/comprehension performance is relatively resistant to unilateral damage and shows rapid recovery (because the function is supported bilaterally), unilateral left ATL damage typically leaves patients with permanent naming impairments. Presumably, this must reflect the fact that, because of its intrinsically lower connectivity to speech-production systems, the right ATL demi-hub is unable to support recovery of naming. This hypothesis was supported by further explorations of the demi-hub model.[12] As previously demonstrated,[48] reducing the connectivity from the right demi-hub to speech-production systems increased the model's reliance on the left demi-hub

for semantically related speech production. In addition, this asymmetric connectivity profile also led to a more limited improvement of naming function in comparison to comprehension in its postdamage recovery phase.

Are graded hemispheric differences a general organizational principle of the temporal lobe?

Intriguingly, this concept of bilateral yet graded representation has also been proposed to govern other cortical areas (see Refs. 19 and 87). When comparing left versus right posterior temporal lobe damage, patients with right vOT lesions often present with face-recognition deficits (prosopagnosia), whereas patients with left vOT damage often present with reading deficits (pure alexia).[114] Careful comparison between these two groups of patients has shown that the right vOT prosopagnosic patients also exhibit mild reading difficulties and that the left vOT pure alexic patients also exhibit mild face-recognition impairments.[114,115] The vOT may therefore be another region in which hemispheric specialization is less modular and more graded than has often been assumed. This pattern of graded laterality has also been shown for medial temporal lobe episodic memory function in studies of patients with left versus right temporal lobe epilepsy. In these investigations, the verbal effect in the left hemisphere is highly replicable, yet the corresponding effect for nonverbal tasks in the right hemisphere is less secure/consistent, with the effect more likely to be bilateral.[116,117] Not only does this replicate the findings from the more lateral ventral ATL for semantic processing,[11] it also suggests that the bilateral yet graded hypothesis could be a general organizational principle throughout the temporal lobe.

Conclusions

The graded, bilateral ATL hub-and-spoke account makes the predictions that (1) both the left and right ATLs are critical for normal semantic processing, and (2) the ATLs are not purely homogeneous in their function, with subtle graded functional differences emerging as a result of differential connectivity.[11,23] This account provides a compromise between theories that posit no differences between the functions of the left and right ATLs and those that posit that the left and right ATLs are each solely responsible for independent functions.[14–17,62,63,72] The principle of the graded hub-and-spoke account is derived from converging sources of evidence and has been exemplified in computational models.[12] This principle, we argue, is not limited to the ATLs but may be a general neurocomputational principle that underlies the organization of the temporal lobes (see Ref. 19).

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Conflicts of interest

The authors declare no conflicts of interest.

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