Establishing task- and modality-dependent dissociations between the semantic and default mode networks

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The default mode network (DMN) and semantic network (SN) are two of the most extensively studied systems, and both are increasingly used as clinical biomarkers in neurological studies. There are strong theoretical reasons to assume a relationship between the networks, as well as anatomical evidence that they might rely on overlapping cortical regions, such as the anterior temporal lobe (ATL) or angular gyrus (AG). Despite these strong motivations, the relationship between the two systems has received minimal attention. We directly compared the SN and DMN using a large ($n = 69$) distortion-corrected functional MRI (fMRI) dataset, spanning a range of semantic and nonsemantic tasks that varied input modality. The results showed that both networks fractionate depending on the semantic nature of the task, stimulus type, modality, and task difficulty. Furthermore, despite recent claims that both AG and ATL are semantic hubs, the two areas responded very differently, with results supporting the role of ATL, but not AG, in semantic representation. Specifically, the left ATL was positively activated for all semantic tasks, but deactivated during nonsemantic task performance. In contrast, the left AG was deactivated for all tasks, with the level of deactivation related to task difficulty. Thus, ATL and AG do not share a common interest in semantic tasks, but, rather, a common "disinterest" in nonsemantic tasks. The implications for the variability in the DMN, its cognitive coherence, and interpretation of resting-state fMRI data are discussed.

semantic network | default mode network | distortion-corrected fMRI | anterior temporal lobe | angular gyrus

Two substantial bodies of research literature, spanning cognitive and clinical neuroscience fields, have been dedicated to exploring the function and components of the semantic network (SN) and the default mode network (DMN). The DMN is an anatomically defined network that shows task-related deactivation during many goal-directed tasks (i.e., rest > task) (1) and can be reliably delineated using techniques such as independent components analysis (ICA) of resting-state functional MRI (fMRI) (2). The SN is a fronto-temporo-parietal network that is sensitive to semantic content in comparisons of semantic tasks > rest/nonsemantic control tasks (3). Although investigations of the DMN and SN have been primarily independent of each other, there are good reasons to compare the two networks directly. First, the networks might share common cognitive functions. One prominent theory suggests that during "rest," the brain is engaged in the activation of rich conceptual representations, and thus default-mode processing places strong demands on the semantic system (4). Secondly, the DMN and SN engage some common anatomical areas. The DMN consistently includes medial prefrontal cortex, parietal areas [angular gyrus (AG), precuneus, posterior cingulate cortex (PCC)], and, somewhat more variably, the lateral anterior temporal lobe (ATL) and hippocampus (1, 5). Some of these areas are considered central to semantic processing. For instance, both the ATL and AG have been proposed to be "semantic hubs" that help to represent

multimodal semantic representations (6–8). However, despite these strong motivations, only a handful of studies have directly compared the two networks; even fewer have (i) used methods to maximize the likelihood of detecting ATL activations (9), and (ii) none have compared results across a range of semantic and nonsemantic tasks to establish the functional generality of each network. Accordingly, we investigated the similarities and differences in the SN and DMN using a large ($n = 69$) distortion-corrected fMRI dataset, spanning a range of semantic and nonsemantic tasks that varied the input modality. By comparing the patterns of task-related activation and deactivation, it proved possible to determine when the networks converge and deviate and to reveal task- and modality-dependent responses in both networks.

Comparison between the DMN and SN is challenging because of apparent inconsistencies in both bodies of literatures. The function of the DMN is a hotly debated issue, with proposed functions including mind wandering, monitoring the external environment, internally directed thought, goal-directed thought, thinking about the past or future, or considering alternative perspectives (1, 5, 10–12). Furthermore, some subcomponents of the DMN—in particular the ATL—are inconsistently reported across studies, leading to suggestions that the DMN might be made up of multiple subsystems, each serving distinct functions (semantic memory, episodic memory, decision making, and

Significance

Functional neuroimaging has established that most cognitive functions are supported by distributed neural networks. Hundreds of studies have investigated the semantic network (SN) and the default mode network (DMN) (neural deactivation when undertaking a variety of tasks). These stable networks are increasingly used as biomarkers in neurological and psychiatric investigations. Despite implicating overlapping neural regions and shared cognitive mechanisms, the relationship between the two networks has received minimal attention. Analyses of a large multitask distortion-corrected functional MRI (fMRI) dataset established that both networks fractionate, depending on the semantic nature of the task, stimulus type, modality, and task difficulty. The implications for the SN, variability in the DMN and its cognitive coherence, and interpretation of resting-state fMRI data are discussed.

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affective and sensory processing) (5, 13–15). The inconsistent involvement of ATL might also relate to a series of methodological challenges associated with imaging this region (9).

There is also a lack of clarity within the SN literature. For instance, semantic processing typically engages a fronto-temporo-parietal network (3); however, the role of certain regions within the network is currently under debate. A wealth of converging evidence from neuropsychology, transcranial magnetic stimulation (TMS), PET, and distortion-corrected fMRI suggests that regions within the ATL are crucial in transmodal semantic representation (16–20). However, it is currently unclear as to whether the AG serves a similar function. A meta-analysis of semantic neuroimaging studies found that the AG consistently exhibited sensitivity to semantic manipulations (3), yet the overall AG activation for semantic tasks is often negative with respect to rest (21, 22). Other evidence is more consistent with a role for dorsal AG/intraparietal sulcus (IPS) in executive aspects of semantic processing, rather than semantic representations per se (23). Secondly, the AG has been implicated in numerous cognitive domains outside of the field of semantic cognition, suggesting a more domain-general cognitive function (attention, episodic memory, numerical processing, and syntax; ref. 24). Indeed, one possibility is that the AG forms part of a domain-general processing network that is involved in "automatic" or "stimulus-driven" task-processes and is anticorrelated with the "executive" dorsal parietal cortex (IPS) (24–26). Together, these inconsistencies in both the current SN and DMN literatures make establishing the relationship between the two networks difficult.

A clearer picture might emerge through direct, within-study comparisons. The few existing single-task investigations have found that certain DMN components can show semantic sensitivity (21, 22, 27, 28). For instance, the AG sometimes shows less deactivation for semantic compared with nonsemantic tasks (22, 27). However, the results across studies have been inconsistent; some studies show widespread overlap across multiple DMN and SN areas (AG, ATL, medial prefrontal cortex, cingulate) (21), whereas others find limited overlap (22, 27, 28). Indeed, across studies, no region has been consistently reported in both networks. In addition to the various factors noted above, the lack of clarity might relate to a failure of existing studies to take into account task-dependent variations, because the networks' neural responses are likely to vary based on factors such as stimulus type, modality, or task difficulty (19, 29–31)—which might be clarified by directly comparing DMN and SN across multiple tasks and modalities. One final limitation of the existing work is the tendency to focus solely on areas of DMN–SN overlap and to ignore any large divergences between the networks. This limitation is important, because if large portions of the SN are not involved in DMN, it questions the core theoretical assumption that the DMN's core function is semantic.

To clarify the relationship between the SN and DMN, we conducted a large-scale investigation of the similarities and differences in the SN and DMN by comparing results from multiple semantic and nonsemantic tasks that varied in stimulus type (words, pictures, environmental sounds, numbers, and pattern matching), task difficulty, and input modality (visual and auditory). Critically, data were acquired by using a distortion-corrected fMRI protocol, promoting detection of signal from all parts of the ATL. By comparing the pattern of task-related activation and deactivation, it was possible to determine where SN and DMN converge and segregate, as well as to reveal task- and modality-dependent responses in the networks. In addition, given their potential pivotal role in semantic cognition, we explored the roles of the ATL and AG in more detail.

Results

The DMN was identified by determining areas with greater activation during rest compared with task periods (rest > task). To determine semantic-dependent variations in the network, this contrast was performed separately for the semantic and nonsemantic tasks, and we looked for commonalities across all tasks. These analyses revealed semantic-variant and -invariant effects (Fig. 1 and Table S1). All results reported below (unless otherwise specified) were thresholded by using a voxel height threshold $P < 0.001$ and cluster-corrected by using family-wise error (FWE) $P < 0.05$. Significant deactivation relative to rest during semantic task performance (rest > semantics) was found in a fronto-temporo-parietal network, which included the bilateral inferior parietal lobe (IPL) [AG and supramarginal gyrus (SMG)], medial structures (PCC and medial frontal cortex), the right ATL, the bilateral auditory cortex [Heschl's gyrus and superior temporal gyrus (STG)], the bilateral hippocampus, and frontal areas (left superior orbital gyrus, bilateral ACC, right middle frontal gyrus, and left insula). The pattern of results for the nonsemantic tasks was similar, but with the notable addition of the ATL and IFG bilaterally (this difference was confirmed to be significant, as reported below). Conjunction analyses confirmed a common pattern of deactivation for semantic and nonsemantic tasks of bilateral IPL (AG, SMG, precuneus, and PCC), right ATL, bilateral auditory cortex (Heschl's gyrus and STG), right hippocampus, and frontal areas (bilateral middle frontal gyrus, left superior orbital gyrus, and left ACC). Thus, certain DMN "components" (ATL and IFG) appear to vary depending on the semantic content of the task, whereas other components are recruited for both task types.

To determine the SN, we examined task-related activations (task > rest) for the semantic tasks and compared these activations to the pattern from the nonsemantic tasks (Fig. 1). Overall, semantic tasks were found to activate a fronto-temporo-parietal network and visual cortex (all semantics > rest). This network included the anterior and posterior temporal cortex (left fusiform gyrus, left temporal pole, and left middle temporal gyrus), frontal areas (bilateral IFG, left precentral gyrus, and right middle orbital gyrus), lateral superior parietal cortex (bilateral IPS/SPL), and left putamen. Note that parts of this network, the left ATL (especially fusiform gyrus) and IFG, were deactivated for the nonsemantic tasks; thus, certain parts of the DMN are sensitive to semantic content. The SN showed some notable differences in activation, as well as some commonalities compared with the nonsemantic tasks. First, similar positive activation for the nonsemantic tasks (nonsemantic > rest) was found in parietal (bilateral IPS and right SMG) and occipital areas; however, little frontal and ATL activation was found compared with the semantic tasks (although there was some restricted recruitment of the left temporal pole). Indeed, these differences between the semantic
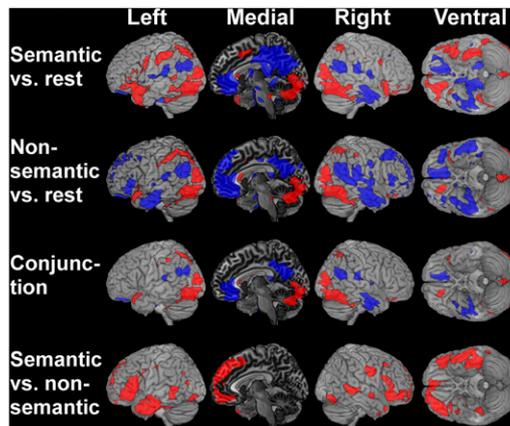

Fig. 1. Positive (red) and negative (blue) activation for semantic tasks vs. rest; the nonsemantic tasks vs. rest; their conjunction; and semantic > nonsemantic tasks (uncorrected, $P < 0.001$).

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and nonsemantic tasks were confirmed by conducting direct comparisons (semantic > nonsemantic), which revealed significantly stronger recruitment of semantic tasks within bilateral IFG, bilateral ATL (temporal pole and fusiform gyrus), bilateral pMTG, and right middle orbital gyrus. A very small cluster within the left AG also showed a stronger response to the semantic compared with nonsemantic tasks; however, this difference was only at a reduced statistical threshold ($P < 0.001$, uncorrected) and, unlike the left ATL, reflected differential deactivation (i.e., greater deactivation for the nonsemantic vs. semantic tasks).

These analyses provide several key findings. First, they show that certain components of the DMN are common to both semantic and nonsemantic tasks, including IPL and medial structures (PCC and medial frontal cortex), as well as right ATL and auditory cortex (although see below). In contrast, other areas of the DMN show task-dependent responses. In particular, the left ATL and bilateral IFG, which are positively activated in the semantic task, form part of the DMN during the performance of nonsemantic tasks (i.e., they are sensitive to both semantics > rest and rest > nonsemantic tasks). Finally, and importantly, the AG and ATL showed dissociable responses. In particular, the left ATL was positively activated for semantic tasks and deactivated for nonsemantic tasks, whereas the AG was deactivated by both semantic and nonsemantic tasks (albeit moderately more strongly for the nonsemantic tasks). Thus, this result provides convincing evidence that the ATL and AG serve distinct cognitive functions.

In the next analysis, we investigated whether the SN and DMN vary depending on the type of semantic task. To perform this analysis, we compared tasks involving written words against pictures (i.e., tasks that share the same modality but differ in verbal vs. nonverbal content; Fig. 2 and Table S1). When including only reading-based semantic tasks, the DMN (rest > reading) and the SN (reading > rest) were similar to that revealed by the general semantic analysis described above: The reading-based tasks activated left ATL relative to rest (fusiform gyrus and temporal pole) but deactivated right ATL. However, the pattern was different for the picture-based semantic tasks, which showed bilateral positive ATL activation (temporal pole and fusiform gyrus) and comparatively little ATL deactivation in either hemisphere. Direct contrasts between reading- and picture-based semantic tasks confirmed that picture tasks showed stronger bilateral ATL engagement (fusiform and inferior temporal gyrus), as well as occipital areas (Fig. S1). In contrast, reading-based tasks engaged left IFG, left pMTG, bilateral superior frontal gyrus, and right hippocampus more strongly compared with picture tasks.
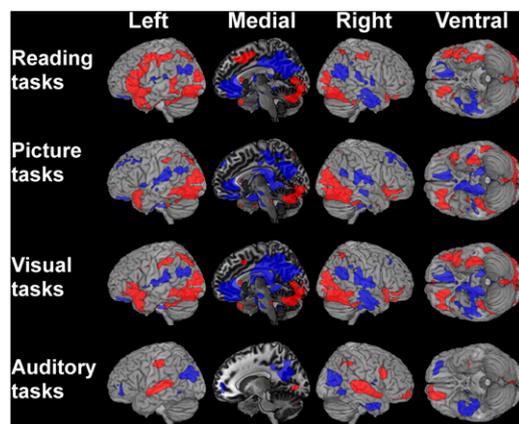

Fig. 2. The effects of stimulus-type and stimulus-modality. Positive (red) and negative (blue) activation for reading tasks vs. rest; picture tasks vs. rest; visual tasks vs. rest; and auditory tasks vs. rest (uncorrected, $P < 0.001$).

Note that the AG showed significant deactivation for both task types, with no significant differences between the two. The medial structures (PCC and medial frontal cortex) were also equivalently deactivated for both tasks. Therefore, these results, combined with those from the more general analysis above, clearly demonstrate that, unlike "core DMN regions" (PCC, medial frontal, and AG), the ATL is involved in both SN and DMN, but its recruitment varies depending on stimulus type.

The influence of input modality was also investigated to examine modality-dependent and -independent responses. In the first overall analysis, auditory cortex was found to form part of the DMN (and this finding was common regardless of the semantic nature of the task). Previous evidence has shown that sensory areas are deactivated when they are not central to task performance (29), and thus we expected that this effect would be modality-dependent, driven mainly by tasks from the visual modality (the majority of tasks). To test this prediction, we separately examined the results for the visual and auditory semantic tasks (Fig. 2). Our predictions were confirmed: The tendency for the auditory cortex to form part of the DMN was driven by the visual tasks (rest > visual tasks). When including only the auditory tasks (rest > auditory tasks), the sensory cortices included in the DMN shifted to include parts of visual rather than auditory cortex. This difference was significant in a direct comparison between the two networks. We also examined areas that were invariant to input modality by conducting a conjunction analysis across visual and auditory semantic tasks. This analysis showed that for the DMN, bilateral ventral parietal cortex (AG and SMG), medial structures (PCC and medial frontal cortex), right ATL, and left superior orbital gyrus were common to visual and auditory tasks (rest > visual and rest > auditory). Conversely, for the SN, the left ATL, pMTG, and IPS were common (visual > rest and auditory > rest).

The analyses reported above confirm that the ATL and AG show a different pattern of activation (and deactivation) to semantic and nonsemantic tasks. To examine the relationship between these areas further, the percent signal change from each region was correlated across tasks. We also examined the relationship between these regions and the IPS, an area that may form an anticorrelated network with the AG (26). Consistent with their profile on the task-based results, the correlation analysis showed no significant relationship between the responses of AG and ATL ($r = -0.34$, $P = 0.18$), providing further evidence that these regions respond dissimilarly. In contrast, a strong negative correlation between IPS and AG was found ($r = -0.64$, $P = 0.006$), consistent with the proposal that the AG and IPS are anticorrelated networks. Additionally, there was a positive trend in the correlation between ATL and IPS activation ($r = 0.45$, $P = 0.07$). Finally, we examined the extent to which activation in each area varied depending on task difficulty by correlating percent signal change with the average RT for the same task. This analysis showed that the AG was negatively correlated with task difficulty ($r = -0.612$, $P = 0.04$), whereas the IPS showed a trend toward a moderate positive correlation ($r = 0.55$, $P = 0.08$), and the ATL showed a positive, but nonsignificant, relationship ($r = 0.51$, $P = 0.11$).

Discussion

The aim of this large-scale (69-participant, multitask) investigation was to clarify the relationship between the DMN and SN. The results indicate that both networks are highly task- and modality-dependent (see summary in Table 1). Certain DMN areas are sensitive to the semantic nature of the task. Specifically, the involvement of ATL regions in the DMN (and left IFG to some extent) was found to vary depending on the level of semantic involvement (semantic vs. nonsemantic) and semantic stimulus type (pictures vs. written words). In particular, these areas were positively activated during semantic tasks, but were deactivated during nonsemantic task performance, and hence form a part of the

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Table 1. Results summary for each region

Region	Task		Stimulus		Modality		Difficulty
	Semantic	Nonsemantic	Written words	Pictures	Visual	Auditory	Correlation
Left ATL	P	N	P	P	P	P	P trend
Right ATL	N	N	N	P	P	N	
AG	N	N	N	N	N	N	N
IPS	P	P	P	P	P	P	P trend
Auditory	N	N	N	N	N	P	
Visual	P	P	P	P	P	N	
Medial structures	N	N	N	N	N	N	

N, negative activation vs. rest; P, positive activation vs. rest.

DMN only for nonsemantic tasks. Activation in other areas was independent of task, but was instead influenced by input modality or task difficulty. Specifically, primary sensory cortices were deactivated for tasks presented in their nonspecialized modality. In contrast, the AG was insensitive to both modality and task, but was more strongly deactivated for more difficult tasks.

Given that both ATL and AG have been proposed as potentially critical regions for the DMN or SN, the second aim of this study was to compare responses in the ATL and AG across tasks. The results showed that the AG and ATL responded very differently to each task, thus implying distinct cognitive functions. In particular, the polarity of activation in the ATL depended on semantic content; it was positively activated for semantic tasks and deactivated for nonsemantic tasks (with laterality varying depending on stimulus type). In contrast, the AG was deactivated by all tasks, with the degree of deactivation relating to task difficulty rather than semantic content per se. Indeed, direct correlations between the AG and ATL activity found no evidence of a significant relationship between the two areas. The AG, unlike the ATL, also showed an inverse relationship with the extent of IPS activation, an area considered central to the "multiple-demand" executive processing system (25, 32).

The present data might have strong implications for interpretation of networks identified in resting-state functional connectivity studies (as revealed by interregional correlations, independent component analysis, etc.). It is understandably the case that the occurrence of positive correlations in functional connectivity between regions is interpreted as evidence of a common underlying cognitive function. For instance, functional connectivity between the ATL, AG, and frontal cortices has been interpreted as evidence of a semantic processing network (33). However, the present data generate a second alternative hypothesis, which can be explored in future studies (e.g., by careful deconstruction of the network components observed in task-dependent ICA; cf. ref. 34). Specifically, the ATL and AG did not show common activation for semantic tasks but, rather, common deactivation during nonsemantic task performance. Accordingly, positive interregional time-course correlations might not reflect a common interest in semantic tasks, but, rather, a common "disinterest" in the tasks that deactivate both regions. If correct, one must be cautious in interpreting the results from connectivity studies alone. Indeed, the present study highlights how cognitive interpretation and fractionation of a distributed network can be aided by combining data from experimentally driven task-based investigations.

The present results suggest that when a neural region is not critical to task function it is deactivated. This finding was true across a variety of structures and processes. For instance, auditory areas were deactivated during visual processing (and vice versa), and semantic areas were deactivated during the performance of nonsemantic tasks. These findings are consistent with two proposals about neural activation. The first is the "limited-capacity" model of neural processing, in which neural resources are finite, and thus alternative cognitive processes are competitive in nature (35). Under these circumstances, the most efficient strategy is to down-regulate a particular neural system if it is unnecessary/disruptive to task performance. Therefore, according to this hypothesis, the changing task dependencies within DMN areas can be explained by variations in the neural computations required for a particular task. The second potentially related proposal is that there are online plasticity mechanisms to balance metabolic energy consumption against task performance (36). Thus, if a region's neurocomputational function is not required for the current task, its activity is down-regulated to save metabolic energy.

By combining data across a variety of different semantic and nonsemantic tasks, we were able to clarify the relationship between the DMN and SN. The overlap was particularly clear for regions within the ATL. These data are consistent with a convergence of results from neuropsychology, TMS, functional neuroimaging, and intracranial recordings, which points to these ATL regions underpinning a transmodal semantic representational hub (7, 8, 16, 20, 37). This outcome is highly consistent with the "semantic hypothesis" for the DMN. Although originally proposed for the AG rather than the ATL, this hypothesis suggests that during rest, the brain is engaged in detailed conceptual-language processes that draw on the SN (4). The response characteristics of the ATL fit perfectly with this hypothesis. It does not seem to hold, however, for other parts of the DMN (including the AG)—many of which are insensitive to the semantic demands of the task and are, instead, influenced by modality or task difficulty.

The present study strongly suggests that, rather than serving one single cognitive function, the DMN is best viewed as a dynamic patchwork reflecting variable deactivation of several subsystems, each serving distinct computations. Indeed, this view is consistent with recent claims that the DMN consists of multiple dissociable, but interacting, components that serve a variety of cognitive function (semantic memory, episodic memory, decision making, and affective and sensory processing) (5, 13–15). In short, although the DMN network is a relatively consistent neuroimaging phenomenon (reproducible across a range of imaging data and types of analysis; cf. ref. 7), it would appear that it is not a coherent, homogeneous cognitive entity.

In addition to the DMN, this study has implications for semantic models. Some theories propose that the AG is a semantic hub, with a function akin to the ATL (3, 6). The results from this study, however, show that the AG and ATL exhibit very different responses across tasks. Although the brain has multiple tertiary association cortices [indeed, both the ATL and AG have been shown to rank among the highest functionally interconnected areas (38)], the present data provide convincing evidence that the ATL and AG serve distinct cognitive functions. These data, combined with the wealth of converging evidence from

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neuropsychology, fMRI, and TMS, provide compelling support for the core role of the ATL, rather than the AG, in semantic representation. Although the present data do not exclude the possibility that the AG is involved in semantic processing in some way, at the very least these results show that the AG does not perform a similar role to the ATL in semantic cognition.

The present results showed that the left ATL was positively engaged during all semantic tasks, whereas the right ATL was sensitive to the stimulus type, with pictures generating positive activation, whereas written words led to deactivation. This finding adds to a growing body of literature comparing processing in the left vs. right ATL. A seminal magnetoencephalography study of semantic processing across modalities, as well as a recent large-scale meta-analysis of functional imaging studies (37, 39), found that ATL activation for written words or speech production is strongly left-lateralized, whereas other forms of semantic tasks (pictures, auditory words, and auditory sounds) show bilateral ATL engagement (see also ref. 19). These and parallel neuro-psychological data on left vs. right ATL differences have been formally considered in a number of implemented computational models of semantic processing (40, 41). The key ideas from these models are that semantic representation may be supported by regions within the ATLs, bilaterally, with differential patterns of activation or impairments in unilateral ATL patients arising from the effects of asymmetric connectivity with input and output areas. Thus, the relatively greater importance of the left ATL for spoken tasks and for written-word comprehension would follow from differentially higher connectivity to left-hemisphere–biased speech production systems (cf. ref. 42) and the left posterior ventral occipitotemporal cortex, which exhibits greater involvement in the visual processes that underpin written-word recognition (43). An alternative hypothesis is that each ATL supports discrete semantic functions (44). Irrespective of the exact cognitive interpretation, this finding has a strong methodological implication for the current semantic neuroimaging literature. By far, the most commonly used form of stimulus in semantic fMRI studies is the written word. Although written words have obvious practical and logistic advantages (visual presentation of stimuli is much easier than auditory in the scanner, and written words allow the full range of concrete, abstract, emotion, etc., concepts to be probed), it is clear that written words—unlike pictures, spoken words, and sounds—generate a strongly left-lateralized pattern of activation. This result could encourage the apparent conclusion that semantic processing is predominantly left-lateralized, when, in fact, for all modalities other than written words, it appears to be much more bilateral in form.

The medial structures (PCC and medial frontal cortex) and AG were found to be deactivated by all task types. This finding is consistent with observations that these regions form the most reliable and highly connected components of the DMN (5, 38, 45) and are considered to be core parts of the DMN (45). The medial structures are particular active in tasks involving auto-biographical memory, theory of mind, and episodic memory retrieval, leading to suggestions that they may be involved in self-projection (projecting oneself to a different context) or internal mentation (self-directed thought) (10, 12).

Finally, the question remains as to the core computation of the AG. The present data showed that: (*i*) the AG is deactivated by semantic and nonsemantic tasks, and the magnitude of deactivation relates to task difficulty; and (*ii*) AG deactivation is anticorrelated with activation of the dorsal parietal cortex (IPS), suggesting that the two networks serve opposing task functions. According to models of attention, dorsal and ventral parietal cortices are involved in top-down vs. bottom-up attentional processes, respectively (46). Thus, it is plausible that dorsal and ventral areas are implicated in (relatively domain-general) executive vs. automatic processing, respectively. With regard to AG's core function, a recent large-scale multidomain meta-

analysis of 386 neuroimaging studies also showed that the AG (*i*) deactivates for a wide variety of domains (including semantic tasks, executively demanding decisions, etc.) but (*ii*) is positively engaged by a variety of different domains (episodic retrieval, numerical tasks, sentence-level tasks, etc.) (24). Thus, it appears that the AG serves a more domain-general function and is not specialized for semantic processing. One possibility is that the parietal cortex acts as a multimodal online buffer of incoming internal or external information (24). Within this system, the dorsal and ventral parietal cortex serve counterpointed roles; the ventral system automatically buffers input, whereas the dorsal system is involved in top-down executive processing of buffered information. Indeed, this hypothesis is consistent with evidence for the role of the parietal cortex in working and short-term memory (47). According to this theory, the continual automatic buffering of additional information by the ventral parietal cortex can be disruptive during the performance of some, but not all, goal-directed executively demanding tasks. Hence, during difficult task performance, activation of this region is suppressed.

Methods

Tasks. Data were collected from seven semantic tasks plus modality- and RT-matched nonsemantic tasks from across four fMRI studies (*n* = 69). Each study included at least one semantic condition and one nonsemantic control condition from the same modality. The tasks are described in detail elsewhere (17–19, 48); however, crucially for the present study, the paired semantic/nonsemantic tasks varied in stimulus type and modality: picture tasks (×2), written word tasks (×3), auditory word tasks (×1), and environmental sounds tasks (×1) (Table 2).

Scanning. Images were acquired on a 3T Philips Achieva scanner by using an eight-element SENSE head coil with a sense factor of 2.5. The data from each study were collected by using the same distortion-corrected fMRI technique (see Table S2 for individual study parameters). Following the standard method for distortion-corrected spin-echo fMRI (49), the images were acquired with a single-direction *k* space traversal and a left–right phase encoding direction. A "prescan" was acquired before each run, consisting of 10 volumes of dual-direction *k* space traversal spin-echo echo-planar imaging scans. This acquisition provided 10 pairs of images matching the functional time series, but with distortions in both phase-encoding directions (10 left–right and 10 right–left). These scans were used in the distortion-correction procedure. The correction was computed by using the method reported in ref. 49, in which each image from functional time series is registered to the mean of the prescan images by using a six-parameter rigid-body transformation. Subsequently, a spatial transformation matrix was calculated from the prescan images, consisting of the spatial remapping necessary to correct the distortion. This transformation was then applied to each of the coregistered functional images.

Analyses. By using SPM5, data were motion-corrected and coregistered to the anatomical T1. Images were then spatially normalized to Montreal Neurological Institute standard space, resampled to $3 \times 3 \times 3$-mm dimensions, and

Table 2. Details of each fMRI task

Study	Task	Stimulus type	Modality
1	Synonym judgment	Words	Visual
	Number judgment	Numbers	Visual
2	Semantic association	Words	Visual
	Semantic association	Pictures	Visual
	Stimulus matching	Scrambled words	Visual
	Stimulus matching	Scrambled pictures	Visual
3	Category judgment	Pictures	Visual
	Category judgment	Words	Auditory
	Category judgment	Sounds	Auditory
	Stimulus matching	Scrambled pictures	Visual
	Auditory decision	Pink noise	Auditory
4	Synonym judgment	Words	Visual
	Number judgment	Numbers	Visual

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smoothed with a Gaussian filter of FHWM = 8 mm. First- and second-level analyses were carried out by using SPM8. At the first level, a general linear model analysis was performed by modeling each condition as a separate regressor using a boxcar function convolved with the canonical hemodynamic response function. Contrasts were calculated for each condition vs. rest (task > rest). In the second-level analysis, all data were entered into a single ANOVA model with each "study" included as a separate level. This method thereby controls for any cross-study confounds. In addition, "subject" was added as a covariate to the model to control for any subject effects. T contrasts were computed to examine overall effects of semantics (semantics > rest, nonsemantic > rest, and semantics > nonsemantics), stimulus type (picture tasks > rest, word tasks > rest, pictures > words, and words > pictures), and modality (visual > rest, auditory > rest, visual > auditory, and auditory > visual). These contrasts-of-interest were computed from the same omnibus ANOVA that modeled both study and subject. Accordingly, the overall model accounts for the variance associated with any study- or subject-specific variations and then reveals the activation differences, which are attributable uniquely to the contrast-of-interest. Unless otherwise stated, a standard voxel height threshold $P < 0.001$, cluster corrected by using FWE $P < 0.05$, was used.

Correlation analyses were performed to determine the relationship between AG, ATL (anterior fusiform gyrus), and IPS activation and task difficulty. Task difficulty was determined based on the average reaction time for each task, across participants. These mean reaction times were then correlated with the participant-average percent signal change from an AG, ATL, and IPS region of interest (ROI). The ROIs were defined based on the voxels showing significant activation for the contrast of semantics > rest (ATL), all tasks > rest (IPS), or rest > all tasks (AG) from the higher-level analysis.

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