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

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Abstract

      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 fMRI dataset, spanning a range of semantic and non-semantic 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 non-semantic 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 non-semantic tasks. The implications for the variability in the DMN, its cognitive coherence and interpretation of resting-state fMRI data are discussed.

Significance statement

      Functional neuroimaging has established that most cognitive functions are supported by a distributed neural network. Hundreds of studies have investigated the semantic network and the default mode network (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 multi-task distortion-corrected 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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<u>Introduction</u>

      Two substantial research literatures, 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 fMRI (2). The SN is a fronto-temporo-parietal network that is sensitive to semantic content in comparisons of semantic tasks > rest/non-semantic 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 multi-modal semantic representations (6-8). However, despite these strong motivations, only a handful of studies have directly compared the two networks and even fewer have (i) utilized methods to maximize the likelihood of detecting ATL activations (9) and (ii) none have compared results across a range of semantic and non-semantic tasks in order 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 non-semantic 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 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 sub-components of the

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DMN, in particular the ATL, are inconsistently reported across studies, leading to suggestions that the DMN might be made up of multiple sub-systems each serving distinct functions (semantic memory, episodic memory, decision making, 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, 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/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, syntax: 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 anti-correlated 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 to non-semantic 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) whilst 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 also relate to a failure of existing studies to take into account task-dependent variations, as 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 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.

In order 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 non-semantic tasks that varied in stimulus-type (words, pictures, environmental sounds, numbers, pattern matching), task-difficulty and input-modality (visual and auditory). Critically, data were acquired 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 pivot 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 to task periods (rest > task). In order to determine semantic-dependent variations in the network, this contrast was performed separately for the semantic and non-semantic tasks, as well as looking for commonalities across all tasks. These analyses revealed semantic-variant and semantic-invariant effects (see Fig.1, and Supplementary Table 1). All results reported below (unless otherwise specified) were thresholded using a voxel height threshold $p < .001$, cluster-corrected using FWE $p < .05$. Significant deactivation relative to rest during semantic task performance (rest > semantics) was found in a fronto-temporo-parietal network, which included bilateral inferior parietal lobe (IPL) (AG, supramarginal gyrus (SMG)), medial structures (PCC and medial frontal cortex), the right ATL, bilateral auditory cortex (Heschl's gyrus and STG), bilateral hippocampus, and frontal areas (left superior orbital gyrus, bilateral ACC, right middle frontal gyrus and left insula). The pattern of results for the non-semantic 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 non-semantic 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 this to the pattern from the non-semantic tasks (see Fig 1). Overall, semantic tasks were found to activate a fronto-temporo-parietal network and visual cortex (all semantics > rest). This included anterior and posterior temporal cortex (left fusiform gyrus, left temporal pole, left middle temporal gyrus), frontal areas (bilateral IFG, left precentral gyrus, 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 non-semantic 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 to the non-semantic tasks. Firstly, similar positive activation for the non-semantic tasks (non-semantic > rest) was found in parietal (bilateral IPS, right SMG) and occipital areas, however little frontal and ATL activation was found compared to the semantic tasks (although there was some restricted recruitment of the left temporal pole). Indeed these differences between the semantic and non-semantic tasks were confirmed by conducting direct comparisons (semantic > non-semantic), 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 to non-semantic tasks, however, this difference was only at a reduced statistical threshold (p < .001, uncorrected) and, unlike the left ATL, reflected differential deactivation (i.e. greater deactivation for the non-semantic vs. semantic tasks).

These analyses provide several key findings. First, they show that certain components of the DMN are common to both semantic and non-semantic tasks, including IPL, 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, left ATL and bilateral IFG, which are positively activated in the semantic task, form part of the DMN during the performance of non-semantic tasks (i.e. they are sensitive to both semantics > rest and rest > non-semantic 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 non-semantic tasks, whereas the AG was deactivated by both semantic and non-semantic tasks (albeit moderately more strongly for the non-semantic

tasks). Thus, this 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 do this we compared tasks involving written words against pictures (i.e. tasks that share the same modality but differ in verbal vs. non-verbal content; see Figure 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 (see Figure S1). In contrast, reading-based tasks engaged left IFG, left pMTG, bilateral superior frontal gyrus, and right hippocampus more strongly compared to picture tasks. 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 modality-independent responses. In the first overall analysis, auditory cortex was found to form part of the DMN (and this 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 (see Figure 2). Our predictions were confirmed: the tendency for 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.

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This showed that for the DMN, bilateral ventral parietal cortex (AG, 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). Whereas 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 non-semantic 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 anti-correlated 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 ($r = -0.34$, $p = .18$), providing further evidence that these regions respond dissimilarly. In contrast, a strong negative correlation between IPS and AG was found ($r = -0.64$, $p = .006$), consistent with the proposal that the AG and IPS are anti-correlated networks. Additionally, there was positive trend in the correlation between ATL and IPS activation ($r = 0.45$, $p = .07$). 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 showed that the AG was negatively correlated with task difficulty ($r = -.612$, $p = .04$), whereas the IPS showed a trend towards a moderate positive correlation ($r = .55$, $p = .08$), and the ATL showed a positive but non- significant relationship ($r = .51$, $p = .11$).

Discussion

The aim of this large-scale (69 participant, multi-task) 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 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. non-semantic) and semantic stimulus-type (pictures vs. written words). In particular these areas were positively activated during semantic tasks but were deactivated during non-semantic task performance, and hence form a part of the DMN only for non-semantic 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 non-specialised 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 non-semantic 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 current data might have strong implications for interpretation of networks identified in resting state functional connectivity studies (as revealed by inter-regional 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 current 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.(34)). Specifically, the ATL and AG did not show common activation for semantic tasks but rather common deactivation during non-semantic task performance. Accordingly, positive inter-regional time-course correlations might not reflect a common interest in semantic tasks but rather a common "disinterest" in the tasks which deactivate both regions. If correct, one must be cautious in interpreting the results from connectivity studies alone. Indeed, the current study highlights how cognitive interpretation and fractionation of a distributed network can be aided by combining data from experimentally-driven task-based investigations.

The current results suggest that when a neural region is not critical to task function it is deactivated. This 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 non-semantic 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 in order to save metabolic energy.

By combining data across a variety of different semantic and non-semantic 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 ATL, this hypothesis suggests that during 'rest' the brain is engaged in detailed conceptual-language processes that draw on the semantic network (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 current 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, affective and sensory processing)(5, 13-15). In short, whilst the DMN network is a relatively consistent neuroimaging phenomenon (reproducible across a range of imaging data and types of analysis: cf. [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. Whilst the brain has multiple tertiary association cortices (indeed both the ATL and AG have been shown to rank amongst the highest functionally interconnected areas (38)), the current data provide convincing evidence that the ATL and AG serve distinct cognitive functions. These data, combined with the wealth of converging evidence from

neuropsychology, fMRI and TMS provides compelling support for the core role of the ATL, rather than AG, in semantic representation. Although the current 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 current 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 adds to a growing literature comparing processing in the left vs. right ATL. A seminal MEG 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-lateralised, whereas other forms of semantic tasks (pictures, auditory words, and auditory sounds) show bilateral ATL engagement (see also 19). These and parallel neuropsychological data on left vs. right ATL differences, have been formally considered in a number 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 productions systems (cf. 42) and 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. Whilst this has 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 generates a strongly left-lateralised pattern of activation. This could encourage the apparent conclusion that semantic processing is predominately left-lateralised 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 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 autobiographical 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 current data showed that: (1) the AG is deactivated by semantic and non-semantic tasks, and the magnitude of deactivation relates to task-difficulty; and (2) AG deactivation is anti-correlated with activation of the dorsal parietal cortex (IPS) suggesting that two networks serve opposing task functions. According to models of attention, dorsal and ventral parietal cortex as 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 multi-domain meta-analysis of 386 neuroimaging studies also showed that the AG (a) deactivates for a wide variety of domains (including semantic tasks, executively demanding decisions, etc.) but (b) 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 specialised for semantic processing. One possibility is that the parietal cortex acts as a multi-modal 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 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 7 semantic tasks plus modality- and RT-matched non-semantic tasks from across four fMRI studies (N = 69). Each study included at least one semantic condition and one non-semantic 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/non-semantic tasks varied in stimulus-type and modality; picture tasks

(×2), written word tasks (×3), auditory word tasks (×1), and environmental sounds tasks (×1) (see Table 2).

Scanning: Images were acquired on a 3T Philips Achieva scanner using an 8 element SENSE head coil with a sense factor of 2.5. The data from each study were collected using the same distortion-corrected fMRI technique (see Supplementary Material 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 "pre-scan" was acquired before each run, consisting of 10 volumes of dual direction *k* space traversal SE EPI scans. This 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 using the method reported by (49) in which each image from functional time-series is registered to the mean of the pre-scan images using a 6-parameter rigid-body transformation. Subsequently, a spatial transformation matrix is calculated from the pre-scan images, consisting of the spatial re-mapping necessary to correct the distortion. This transformation was then applied to each of the co-registered functional images.

Analyses: Using SPM5, data were motion-corrected and co-registered to the anatomical T1. Images were then spatially normalised to MNI standard space, resampled to 3 x 3 x 3 mm dimensions, and smoothed with a Gaussian filter of FHWM = 8mm. First- and second-level analyses were carried out 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 HRF. 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 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, non-semantic > rest, and semantics > non-semantics), 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 which modelled 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 $p < .001$, cluster corrected using FWE $p < .05$ was used.

Correlation analyses were performed in order to determine the relationship between AG, ATL (anterior fusiform gyrus) and IPS activation and task-difficulty. Task-difficulty was determined based on the average RT for each task, across participants. These RT data 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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Figure Legends

Fig. 1. Positive (red) and negative (blue) activation for: semantic tasks vs. rest; the non-semantic tasks vs. rest; their conjunction; and semantic > nonsemantic tasks (uncorrected, p < .001).

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 < .001).

	Left	**Medial**	**Right**	**Ventral**
Semantic vs. rest				
Non-semantic vs. rest				
Conjunc-tion				
Semantic vs. non-semantic				

	Left	Medial	Right	Ventral
Reading tasks				
Picture tasks				
Visual tasks				
Auditory tasks				
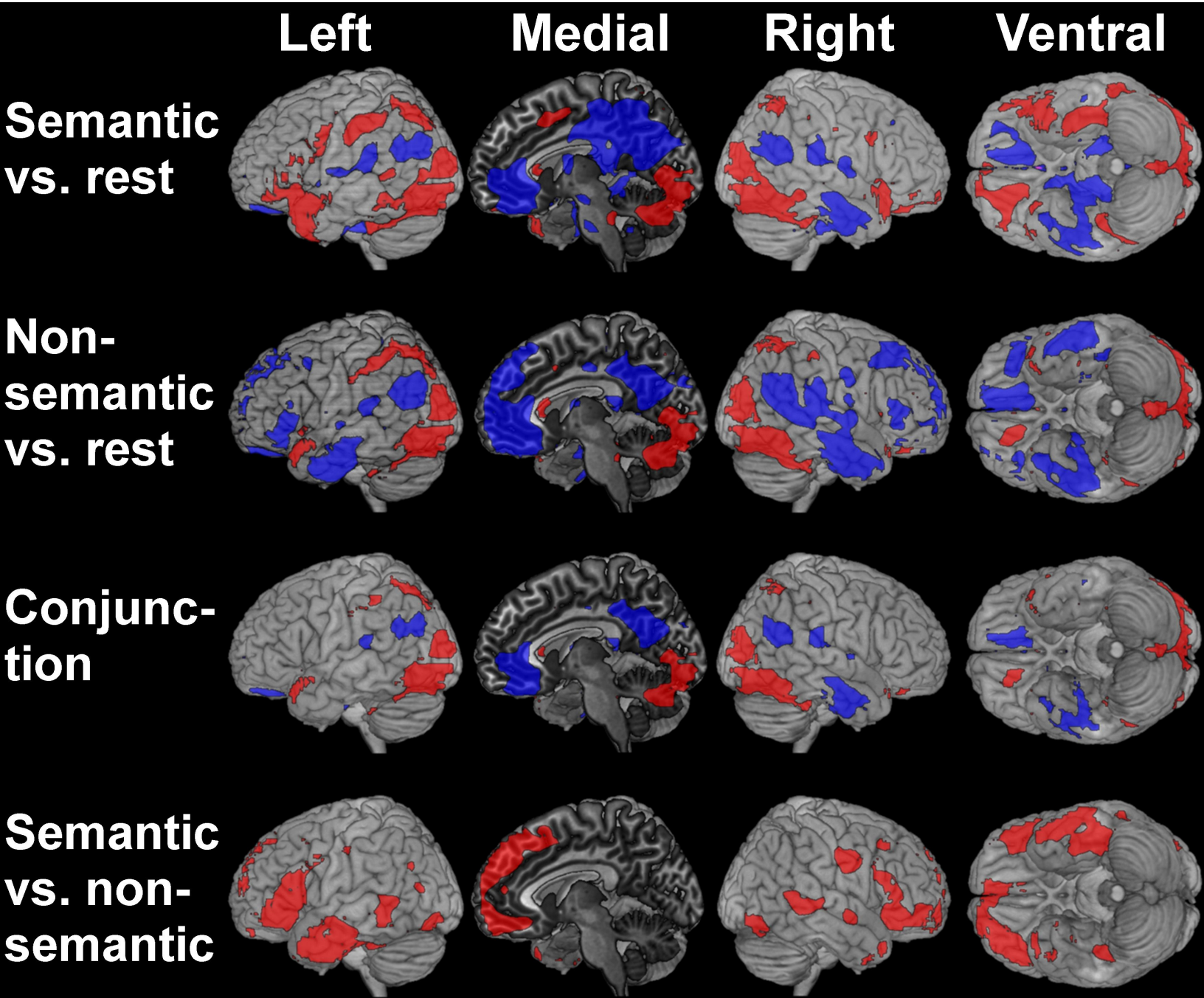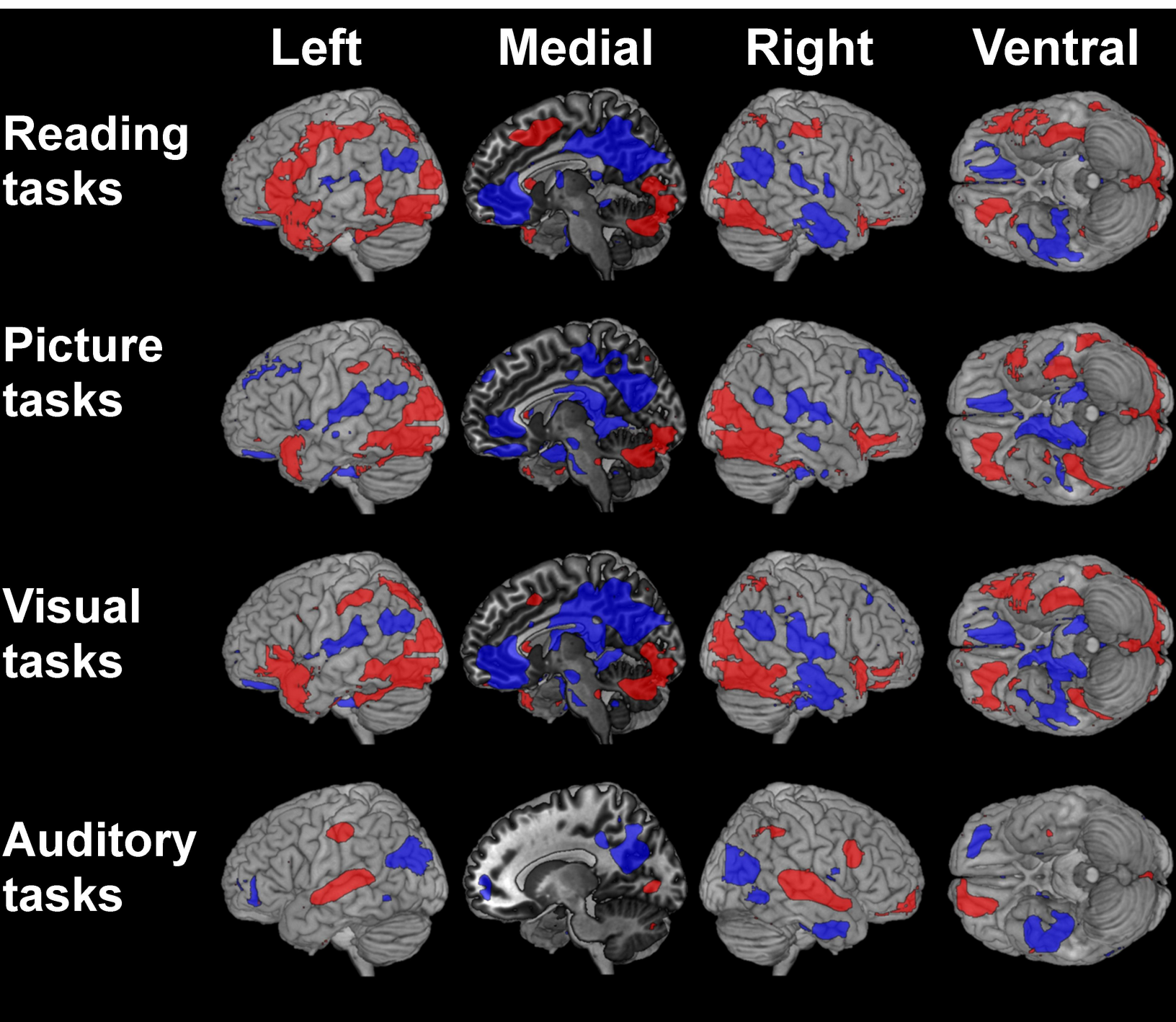
Table 1: Results summary for each region (P = positive activation vs. rest, N = negative activation vs. rest).

	Task		Stimulus		Modality		Difficulty
	Semantic	*Non-semantic*	*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	

Table 2. Details of each fMRI task.

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

Figure S1. The direct contrast of picture tasks and reading tasks showing greater right ATL activation (fusiform and inferior temporal gyrus) for the picture tasks (red = pictures > reading, blue = reading > pictures (uncorrected, p < .001)).
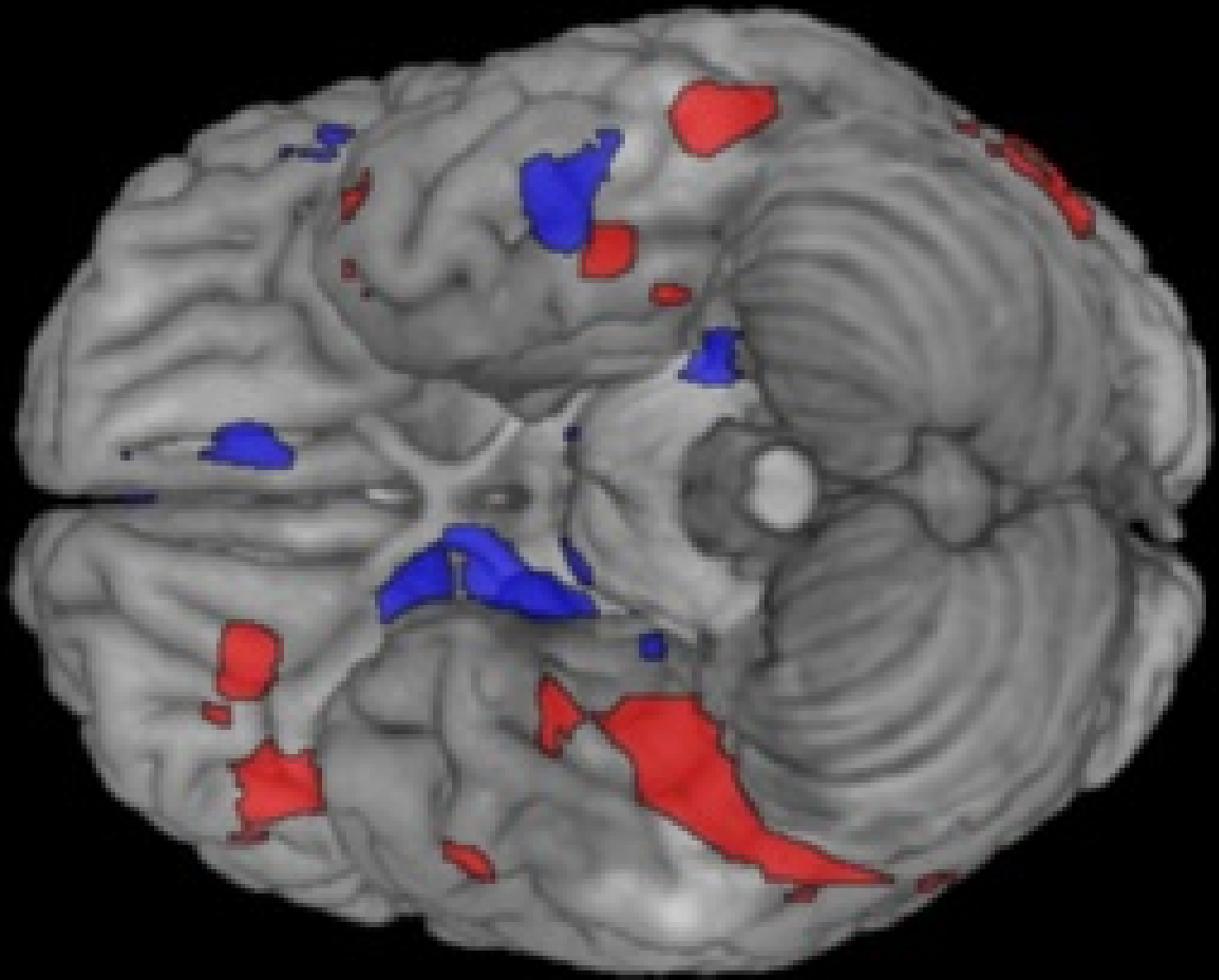
Table S1. The results from the cluster corrected analysis thresholded at a voxel height of p=0.001 (FWE cluster corrected at p=0.05).

Contrast		Cluster	T	x	y	z
Semantic tasks > rest	Left inferior occipital gyrus	6888	20.55	-36	-87	-12
	Left inferior occipital gyrus		20.29	-33	-90	-9
	Left inferior occipital gyrus		19.66	-27	-93	-6
	Right inferior occipital gyrus		19.38	36	-87	-6
	Right inferior occipital gyrus		17.84	42	-84	-9
	Left inferior occipital gyrus		17.59	-39	-72	-12
	Left lingual gyrus		16.68	-24	-90	-18
	Left inferior occipital gyrus		16.21	-18	-93	-12
	Left middle occipital gyrus		14.91	-33	-93	6
	Right fusiform gyrus		14.00	42	-63	-18
	Right fusiform gyrus		13.46	33	-66	-12
	Right cerebellum		10.71	27	-51	-27
	Right cerebellum		10.68	30	-54	-30
	Right fusiform gyrus		10.51	42	-36	-27
	Left fusiform gyrus		9.81	-36	-9	-30
	Right cerebellum		9.66	9	-72	-30
	Left postcentral gyrus		8.34	-42	-30	45
	Left intraparietal sulcus		8.96	-30	-60	45
	Left superior occipital gyrus		9.25	-30	-72	27
	Right intraparietal sulcus		8.57	30	-60	42
	Left temporal pole	323	8.31	-57	12	-12
	Left medial temporal pole		8.05	-42	21	-36
	Left frontal pole		6.05	-48	45	-12
	Right temporal pole	306	8.06	30	24	-36
	Right temporal pole		6.64	45	27	-21
	Left precentral gyrus	402	7.90	-36	6	30
	Left precentral gyrus		5.16	-27	-9	45
	Left precentral gyrus		4.14	-54	3	39
	Right middle orbital gyrus	177	7.50	24	42	-18
	Left rectal gyrus		5.77	0	60	-18
	Right superior orbital gyrus		4.96	12	66	-15
	Right SMA	138	7.36	9	12	48
	Left SMA		5.21	-6	12	45
	Left SMA		3.86	-9	3	51
	Right inferior frontal gyrus, pars opercularis	105	5.01	39	6	30
	Right inferior frontal gyrus, pars triangularis		3.84	42	27	21
	Right middle frontal gyrus		3.79	39	3	39
	Left putamen	102	4.96	-24	6	-3
	Left thalamus		4.30	-12	-15	3
	Left putamen		3.97	-21	0	6
Rest > semantic tasks	Left precuneus	7810	11.84	-6	-63	27

	Left precuneus		11.56	-30	-57	6
	Left calcarine gyrus		11.08	-9	-69	21
	Right precuneus		10.68	6	-60	24
	Right precuneus		10.43	9	-57	27
	Right middle cingulate cortex		10.30	9	-39	39
	Right middle cingulate cortex		9.99	3	-33	39
	Left precuneus		9.67	-15	-45	15
	Right cuneus		9.54	15	-69	24
	Left Heschl's gyrus		9.51	-42	-21	6
	Right precuneus		8.92	24	-48	15
	Right supramarginal gyrus		8.59	45	-36	21
	Right Heschl's gyrus		8.51	45	-18	6
	Left ACC		8.22	-6	33	-3
	Left ACC		8.15	-9	42	-3
	Right superior temporal gyrus		7.86	54	-30	18
	Left angular gyrus		6.94	-42	-75	30
	Left angular gyrus		5.31	-51	-57	24
	Left supramarginal gyrus		6.96	-48	-30	12
	Right angular gyrus		7.31	54	-57	21
	Left middle frontal gyrus	152	6.11	-27	24	36
	Right middle frontal gyrus	140	5.67	27	27	36
	Right superior frontal gyrus		4.03	24	18	42
	Right superior frontal gyrus		3.75	21	21	51
Non-semantic tasks > rest	Left middle occipital gyrus	6141	15.53	-30	-93	-6
	Right inferior occipital gyrus		15.04	36	-90	-6
	Right inferior occipital gyrus		14.80	33	-87	-3
	Right inferior occipital gyrus		13.85	30	-84	-9
	Left middle occipital gyrus		13.77	-33	-93	6
	Left lingual gyrus		12.83	-27	-84	-15
	Left inferior occipital gyrus		12.48	-42	-69	-9
	Right inferior occipital gyrus		12.26	42	-84	-9
	Left lingual gyrus		12.16	-24	-90	-18
	Right lingual gyrus		12.05	15	-90	-9
	Right lingual gyrus		11.92	21	-90	-9
	Left middle occipital gyrus		11.54	-30	-72	27
	Left middle occipital gyrus		11.01	-36	-90	18
	Right superior occipital gyrus		9.64	30	-63	39
	Right fusiform gyrus		9.62	45	-63	-18
	Cerebellar vermis		8.78	0	-69	-30
	Left intraparietal sulcus		8.04	-39	-39	39
	Left superior parietal lobule		8.62	-27	-63	45
	Right intraparietal sulcus		5.73	42	-39	42
	Left precentral gyrus	81	4.65	-36	0	33
	Left rolandic operculum		4.15	-45	0	12
Rest > non-semantic tasks	Right middle temporal gyrus	3650	8.40	57	-15	-15

	Right middle temporal gyrus		8.29	48	3	-27
	Right hippocampus		7.69	33	-12	-42
	Right middle temporal gyrus		7.64	54	-57	21
	Right supramarginal gyrus		7.44	45	-36	21
	Right precuneus		7.42	27	-48	15
	Left precuneus		7.34	3	-57	30
	Left precuneus		7.05	-3	-60	27
	Right inferior temporal gyrus		6.94	51	-18	-30
	Right cuneus		6.51	9	-72	27
	Right cuneus		6.17	15	-69	24
	Left posterior cingulate cortex		6.04	-9	-51	33
	Left middle cingulate cortex		5.99	-6	-36	39
	Right middle cingulate cortex		5.93	12	-39	39
	Left ACC	2795	8.19	-9	33	-9
	Left rectal gyrus		7.96	-6	42	-24
	Left middle orbital gyrus		7.82	-9	42	-6
	Left superior orbital gyrus		7.33	-12	57	-21
	Left middle frontal gyrus		5.63	-27	24	39
	Right superior frontal gyrus		5.42	21	39	36
	Right superior frontal gyrus		5.23	24	21	45
	Left superior medial gyrus		5.14	-6	54	36
	Right superior medial gyrus		4.91	12	66	15
	Right inferior frontal gyrus, pars triangularis		4.73	51	33	9
	Left superior frontal gyrus		4.54	-15	39	39
	Right middle frontal gyrus		4.52	39	21	45
	Right superior frontal gyrus		4.25	15	57	27
	Right middle orbital gyrus		4.21	33	57	-3
	Right inferior frontal gyrus, pars orbitalis		4.14	51	33	-3
	Right superior medial gyrus		4.11	6	57	36
	Left angular gyrus	492	7.74	-42	-63	24
	Left angular gyrus		7.49	-45	-69	30
	Left supramarginal gyrus		5.04	-45	-45	24
	Left inferior temporal gyrus	630	6.87	-54	-18	-36
	Left medial temporal pole		6.23	-45	9	-33
	Left middle temporal gyrus		5.65	-57	-15	-12
	Left inferior frontal gyrus, pars triangularis	146	5.91	-51	27	6
	Left inferior frontal gyrus, pars orbitalis		5.71	-45	33	-15
	Left inferior frontal gyrus, pars orbitalis		4.74	-33	39	-15
Semantic tasks > non-semantic tasks	Left inferior frontal gyrus, pars triangularis	522	8.66	-54	27	6
	Left inferior frontal gyrus, pars orbitalis		8.12	-45	33	-15

Region	Cluster size	t	x	y	z
Left inferior frontal gyrus, pars orbitalis		7.91	-51	39	-6
Left inferior temporal gyrus	1398	7.91	-42	-24	-27
Left inferior temporal gyrus		7.68	-39	-27	-24
Left middle temporal gyrus		7.27	-54	-42	-9
Left fusiform gyrus		7.19	-39	-36	-21
Left medial temporal pole		6.94	-51	9	-36
Left medial temporal pole		6.86	-51	15	-33
Left fusiform gyrus		6.41	-42	-51	-18
Left middle temporal gyrus		6.04	-66	-15	-24
Left middle temporal gyrus		5.76	-57	0	-33
Left inferior temporal gyrus		5.64	-60	-3	-30
Left middle temporal gyrus		5.58	-48	-21	-9
Left inferior temporal gyrus		5.50	-63	-12	-27
Left inferior temporal gyrus		5.35	-57	-9	-36
Left inferior occipital gyrus		4.46	-39	-84	-12
Left fusiform gyrus		4.22	-39	-72	-15
Left middle temporal gyrus		3.91	-60	3	-15
Left rectal gyrus	1268	6.03	-3	57	-15
Right inferior frontal gyrus, pars orbitalis		6.02	48	33	-6
Right middle orbital gyrus		5.87	39	45	-15
Right inferior frontal gyrus, pars orbitalis		5.68	45	33	-15
Right inferior frontal gyrus, pars orbitalis		5.54	42	36	-18
Right inferior frontal gyrus, pars orbitalis		5.51	48	39	-15
Right middle orbital gyrus		4.93	24	66	-9
Left middle orbital gyrus		4.75	-6	33	-12
Left superior frontal gyrus		4.68	-9	54	42
Left superior medial gyrus		4.67	-6	66	15
Right superior orbital gyrus		4.63	15	63	-18
Right middle orbital gyrus		4.62	9	66	-12
Right superior medial gyrus		4.54	12	69	15
Left superior medial gyrus		4.43	-6	42	36
Right inferior frontal gyrus, pars triangularis		4.38	51	21	21
Left superior medial gyrus		4.35	-6	39	45
Right superior temporal gyrus	318	5.82	51	-27	-3
Right middle temporal gyrus		5.14	51	-39	3
Right middle temporal gyrus		4.59	66	-39	0
Right inferior temporal gyrus	96	4.99	45	-33	-21
Right fusiform gyrus		4.80	42	-42	-18
Right postcentral gyrus	85	3.91	60	0	33
Right postcentral gyrus		3.63	57	-12	39

Conjunction: (semantic > rest) & (non-semantic > rest)	Left middle occipital gyrus	5273	15.53	-30	-93	-6
	Right inferior occipital gyrus		15.04	36	-90	-6
	Right inferior occipital gyrus		14.80	33	-87	-3
	Right inferior occipital gyrus		13.85	30	-84	-9
	Left middle occipital gyrus		13.77	-33	-93	6
	Left lingual gyrus		12.83	-27	-84	-15
	Left inferior occipital gyrus		12.48	-42	-69	-9
	Right inferior occipital gyrus		12.26	42	-84	-9
	Left lingual gyrus		12.16	-24	-90	-18
	Right lingual gyrus		12.05	15	-90	-9
	Right lingual gyrus		11.92	21	-90	-9
	Right fusiform gyrus		9.62	45	-63	-18
	Left middle occipital gyrus		9.25	-30	-72	27
	Cerebellar vermis		8.65	0	-72	-30
	Left superior parietal lobule		8.62	-27	-63	45
	Left intraparietal sulcus		7.37	-42	-36	42
	Right intraparietal sulcus		8.57	30	-60	42
	Right angular gyrus		8.57	30	-60	42
Conjunction: (rest > semantic) & (rest > non-semantic)	Left ACC	658	7.68	-9	42	-3
	Left ACC		7.18	-9	33	-6
	Left superior orbital gyrus		6.87	-9	39	-24
	Left precuneus	2283	7.46	-15	-45	15
	Right supramarginal gyrus		7.44	45	-36	21
	Right precuneus		7.42	27	-48	15
	Left precuneus		7.34	3	-57	30
	Right angular gyrus		7.31	54	-57	21
	Left lingual gyrus		7.23	-27	-57	6
	Left precuneus		7.05	-3	-60	27
	Right cuneus		6.51	9	-72	27
	Right cuneus		6.17	15	-69	24
	Left posterior cingulate cortex		6.04	-9	-51	33
	Left middle cingulate cortex		5.99	-6	-36	39
	Right middle cingulate cortex		5.93	12	-39	39
	Right middle cingulate cortex		5.57	6	-45	33
	Right superior temporal gyrus		5.24	42	-21	3
	Left middle cingulate cortex		4.72	0	-12	42
	Right middle cingulate cortex		4.71	3	-21	39
	Right middle temporal gyrus	499	7.14	45	6	-27
	Right hippocampus		6.74	33	-12	-42
	Right middle temporal gyrus		6.66	60	-15	-15
	Left angular gyrus	356	6.48	-42	-72	30
	Left angular gyrus		5.31	-51	-57	24
	Left supramarginal gyrus		4.90	-45	-45	24

	Left supramarginal gyrus		4.84	-48	-33	15
	Left middle frontal gyrus	133	5.63	-27	24	39
	Right middle frontal gyrus	127	5.02	27	27	39
	Right superior frontal gyrus		4.03	24	18	42
	Right superior frontal gyrus		3.75	21	21	51
Reading tasks > rest	Left inferior occipital gyrus	6523	19.56	-27	-93	-6
	Left inferior occipital gyrus		19.44	-33	-90	-9
	Right inferior occipital gyrus		19.27	36	-87	-6
	Left inferior occipital gyrus		17.83	-18	-93	-12
	Right middle occipital gyrus		15.22	27	-93	3
	Left inferior occipital gyrus		14.75	-39	-72	-12
	Left lingual gyrus		14.74	-24	-90	-18
	Left middle occipital gyrus		12.05	-30	-93	6
	Left superior parietal lobule		10.58	-27	-63	45
	Left precentral gyrus		10.05	-39	9	30
	Right cerebellum		9.77	9	-72	-30
	Right fusiform gyrus		9.72	42	-63	-18
	Left inferior temporal gyrus		9.36	-39	-48	-18
	Left inferior parietal sulcus		9.25	-30	-57	48
	Left inferior temporal gyrus		9.13	-39	-15	-33
	Left middle occipital gyrus		8.86	-30	-72	27
	Left postcentral gyrus		7.02	-42	-33	45
	Right intraparietal sulcus		7.28	30	-51	48
	Right middle cingulate cortex	378	8.36	9	15	45
	Left SMA		6.76	-9	12	45
	Left SMA		4.16	-9	3	54
	Right postcentral gyrus	197	5.77	48	-27	48
	Right precentral gyrus		5.57	33	-3	48
	Right postcentral gyrus		4.10	57	-21	51
Rest > reading tasks	Right precuneus	5040	10.55	9	-57	24
	Right middle cingulate cortex		9.98	9	-39	39
	Left lingual gyrus		9.87	-30	-57	3
	Right middle cingulate cortex		9.62	3	-33	39
	Left precuneus		9.46	-9	-57	36
	Left cuneus		9.29	-6	-63	24
	Left lingual gyrus		8.86	-30	-45	-3
	Left calcarine gyrus		8.18	-18	-63	18
	Left superior temporal gyrus		8.04	-42	-36	15
	Left superior temporal gyrus		7.27	-42	-24	6
	Right cuneus		7.11	12	-72	27
	Right middle temporal gyrus		7.08	57	-15	-15
	Right middle temporal gyrus		7.00	51	0	-27
	Left precuneus		6.73	-18	-48	12
	Right middle temporal gyrus		6.66	45	-54	21
	Right superior temporal gyrus		6.61	48	-33	21

	Left angular gyrus		6.41	-42	-75	27
	Left angular gyrus		5.72	-48	-54	24
	Right angular gyrus		6.19	54	-60	24
	Right angular gyrus		5.01	45	-66	33
	Right inferior temporal gyrus		6.05	48	-18	-30
	Right angular gyrus		5.80	45	-75	24
	Left ACC	781	7.70	-6	33	-3
	Left superior orbital gyrus		5.69	-12	57	-6
	Left rectal gyrus		5.37	-9	33	-21
	Right thalamus	115	5.01	3	-15	3
	Left caudate nucleus		3.87	-15	21	6
Picture tasks >rest	Right middle occipital gyrus	6018	16.09	33	-87	0
	Right fusiform gyrus		14.94	30	-66	-12
	Right fusiform gyrus		14.81	36	-57	-12
	Right fusiform gyrus		14.03	39	-54	-15
	Right fusiform gyrus		13.84	30	-81	-6
	Left middle occipital gyrus		13.75	-33	-93	6
	Left inferior occipital gyrus		13.32	-42	-69	-12
	Right inferior occipital gyrus		12.56	42	-78	-12
	Left middle occipital gyrus		12.55	-36	-90	-3
	Left middle occipital gyrus		12.29	-30	-87	12
	Right inferior temporal gyrus		12.26	48	-72	-9
	Left inferior occipital gyrus		12.19	-45	-81	-9
	Left inferior occipital gyrus		11.94	-42	-78	-3
	Left lingual gyrus		11.77	-21	-87	-12
	Left fusiform gyrus		11.59	-30	-72	-15
	Right fusiform gyrus		10.52	42	-36	-27
	Left inferior temporal gyrus	189	8.43	-39	-15	-30
	Left temporal pole	118	6.80	-42	24	-30
	Left temporal pole		5.74	-48	21	-18
	Left temporal pole		5.40	-33	24	-30
	Right superior orbital gyrus	341	6.10	24	39	-15
	Right temporal pole		4.94	57	18	-6
	Right inferior frontal gyrus, pars orbitalis		4.78	45	36	-12
Rest > picture tasks	Left precuneus	5563	12.37	-30	-57	6
	Right precuneus		9.47	27	-48	15
	Left cuneus		8.41	-9	-72	24
	Left superior temporal gyrus		8.05	-42	-36	15
	Right rolandic operculum		7.96	45	-33	21
	Right cuneus		7.61	12	-72	27
	Right precuneus		7.36	6	-60	24
	Right superior temporal gyrus		7.13	54	-30	18
	Right Heschl's gyrus		7.07	42	-21	12
	Right hippocampus		6.98	27	-24	-12
	Right cuneus		6.97	15	-69	24

Contrast	Region	Size	Peak	x	y	z
	Left hippocampus		6.91	-21	-27	-9
	Left Heschl's gyrus		6.84	-39	-24	6
	Right precuneus		6.79	6	-54	33
	Left lingual gyrus		6.22	-12	-39	0
	Left angular gyrus		3.80	-45	-69	30
	Left angular gyrus		4.51	-45	-60	27
	Left superior orbital gyrus	100	6.90	-9	39	-24
	Left superior orbital gyrus		5.42	-9	54	-24
	Right superior frontal gyrus	790	5.82	21	45	36
	Right middle frontal gyrus		5.16	27	27	45
	Left middle frontal gyrus		5.07	-30	30	42
	Right angular gyrus	80	5.18	51	-54	24
Reading > pictures	Left precuneus	301	6.77	-30	-54	12
	Left superior frontal gyrus	1189	5.21	-15	48	42
	Right superior frontal gyrus		5.12	24	48	39
	Left superior medial gyrus		4.82	-3	27	45
	Left middle frontal gyrus		4.66	-48	18	42
	Left middle frontal gyrus		4.48	-45	24	45
	Left SMA		4.47	-6	12	54
	Left middle frontal gyrus		4.31	-30	33	48
	Left postcentral gyrus		4.24	-54	-6	48
	Left inferior frontal gyrus, pars triangularis		3.98	-42	15	30
	Left precentral gyrus		3.91	-45	0	54
	Left inferior frontal gyrus, pars triangularis		3.84	-51	27	18
	Left inferior frontal gyrus, pars triangularis		3.82	-48	24	21
	Left inferior frontal gyrus, pars triangularis		3.81	-54	21	21
	Right superior medial gyrus		3.80	12	36	54
	Right superior medial gyrus		3.80	9	60	33
	Left middle frontal gyrus		3.78	-36	42	36
	Left middle temporal gyrus	198	5.04	-54	-42	3
	Left middle temporal gyrus		4.85	-48	-33	-3
	Left superior temporal gyrus		3.91	-57	0	-12
	Left lingual gyrus	123	4.85	-9	-39	0
	Left hippocampus		4.72	-21	-24	-9
	Right parahippocampal gyrus	174	4.80	15	3	-15
	Right parahippocampal gyrus		4.39	12	-6	-27
	Right superior temporal gyrus	132	4.52	45	-18	3
	Right Heschl's gyrus		4.49	42	-21	12
	Right rolandic operculum		3.93	60	-15	15
Pictures>reading	Right fusiform gyrus	1878	12.65	33	-54	-12
	Right middle occipital gyrus		9.95	42	-81	9

	Right inferior temporal gyrus		9.06	51	-66	-6
	Right fusiform gyrus		7.19	36	-27	-24
	Right fusiform gyrus		7.15	39	-33	-21
	Right superior occipital gyrus		5.33	24	-93	18
	Right angular gyrus		4.66	30	-60	39
	Right middle occipital gyrus		4.54	33	-63	36
	Right superior occipital gyrus		3.99	27	-69	33
	Left fusiform gyrus	1060	8.51	-30	-57	-12
	Left middle occipital gyrus		8.13	-42	-87	9
	Left inferior occipital gyrus		7.18	-45	-72	-3
	Left middle occipital gyrus		7.00	-36	-78	3
	Left middle occipital gyrus		5.76	-30	-93	15
	Left middle occipital gyrus		5.65	-27	-96	18
	Left middle occipital gyrus		5.37	-30	-84	15
	Left cerebellum		3.89	-12	-69	-27
	Left middle occipital gyrus		3.83	-30	-72	30
	Right inferior frontal gyrus, pars orbitalis	84	4.56	42	33	-12
	Right superior orbital gyrus		4.01	24	39	-15
	Right frontal pole		3.90	33	36	-3
Visual tasks > rest	Right inferior occipital gyrus	6691	21.09	33	-87	-3
	Left inferior occipital gyrus		19.37	-27	-93	-6
	Left inferior occipital gyrus		18.15	-36	-84	-12
	Left inferior occipital gyrus		17.53	-39	-72	-12
	Left middle occipital gyrus		16.34	-33	-93	6
	Left lingual gyrus		15.38	-24	-90	-18
	Left middle occipital gyrus		15.05	-30	-87	12
	Right fusiform gyrus		14.08	39	-57	-15
	Right fusiform gyrus		14.01	33	-66	-12
	Right fusiform gyrus		11.50	42	-36	-27
	Left middle occipital gyrus		11.43	-30	-72	27
	Left inferior temporal gyrus		10.95	-39	-12	-33
	Left superior parietal lobule		10.66	-27	-63	45
	Cerebellar vermis		10.17	-3	-72	-27
	Right cerebellum		10.07	9	-72	-30
	Right angular gyrus		9.75	30	-60	42
	Left intraparietal sulcus		7.13	-45	-39	45
	Left precentral gyrus	343	8.81	-39	9	30
	Left precentral gyrus		5.08	-27	-6	45
	Left temporal pole	318	7.89	-45	21	-33
	Left temporal pole		7.42	-57	12	-12
	Left medial temporal pole		7.16	-51	15	-33
	Right temporal pole	290	7.72	30	24	-36
	Right middle orbital gyrus	152	7.02	21	39	-21
	Right inferior frontal gyrus, pars orbitalis		4.56	45	48	-12

	Right inferior frontal gyrus, pars orbitalis		3.92	45	39	-12
Rest > visual tasks	Left precuneus	8326	13.77	-30	-57	6
	Right precuneus		11.26	6	-60	24
	Left cuneus		11.07	-9	-72	24
	Left precuneus		10.25	-6	-63	27
	Left superior temporal gyrus		10.23	-42	-36	15
	Right precuneus		9.80	9	-54	33
	Right cuneus		9.36	12	-72	27
	Right rolandic operculum		9.28	45	-33	21
	Right middle cingulate cortex		9.16	3	-33	39
	Right middle cingulate cortex		8.84	12	-39	39
	Left Heschl's gyrus		8.84	-39	-24	6
	Right cuneus		8.82	15	-69	24
	Left ACC		8.16	-3	30	-3
	Right middle temporal gyrus		7.77	57	-15	-15
	Left angular gyrus		5.41	-45	-72	27
	Right angular gyrus		7.18	48	-54	24
	Right middle frontal gyrus	210	5.10	27	27	42
	Right superior frontal gyrus		5.02	18	42	36
	Right superior frontal gyrus		4.22	21	21	51
	Left middle frontal gyrus	157	5.03	-24	21	42
Auditory tasks > rest	Left middle temporal gyrus	561	9.27	-54	-21	0
	Left middle temporal gyrus		7.33	-57	-36	9
	Right superior temporal gyrus	561	8.50	66	-24	3
	Right superior temporal gyrus		6.81	63	-9	-6
	Right middle temporal gyrus		6.43	45	-39	3
	Right cerebellum	144	6.68	27	-54	-27
	Left postcentral gyrus	272	6.10	-36	-27	45
	Left postcentral gyrus		5.41	-48	-21	45
	Left intraparietal sulcus		4.55	-27	-39	42
	Right middle orbital gyrus	161	5.79	24	51	-15
	Right superior orbital gyrus		4.64	15	63	-18
	Right middle orbital gyrus		4.42	21	66	-12
	Right inferior frontal gyrus, pars triangularis	119	4.68	48	15	24
	Left lingual gyrus	84	4.26	3	-81	0
	Left lingual gyrus		3.81	-12	-78	0
Rest > auditory tasks	Left middle occipital gyrus	255	7.36	-39	-78	27
	Left middle occipital gyrus		5.89	-45	-81	21
	Left middle temporal gyrus		4.56	-57	-63	21
	Left angular gyrus		3.81	-45	-60	24
	Left cuneus	1477	7.24	-6	-66	27
	Right middle cingulate cortex		6.36	9	-36	39
	Left inferior occipital gyrus		5.88	36	-63	12
	Right precuneus		5.81	12	-54	18

	Right middle occipital gyrus		5.50	42	-78	24
	Left posterior cingulate cortex		5.50	-3	-48	27
	Right precuneus		5.49	9	-57	21
	Right middle temporal gyrus		5.28	39	-57	9
	Right middle occipital gyrus		5.06	42	-81	12
	Left precuneus		4.94	-6	-60	45
	Left superior frontal gyrus	240	5.90	-18	54	3
	Left middle frontal gyrus		4.83	-36	48	3
	Right inferior temporal gyrus	355	5.83	57	-3	-33
	Right inferior temporal gyrus		4.56	42	3	-30
	Right parahippocampal gyrus		4.40	33	-36	-12
Visual > auditory	Right inferior occipital gyrus	5292	17.61	33	-87	-3
	Left inferior occipital gyrus		15.53	-27	-93	-6
	Left inferior occipital gyrus		15.45	-24	-90	-9
	Left inferior occipital gyrus		14.26	-36	-84	-12
	Left middle occipital gyrus		14.16	-33	-93	9
	Left inferior occipital gyrus		13.52	-39	-72	-12
	Left middle occipital gyrus		13.08	-30	-87	12
	Right fusiform gyrus		12.42	39	-57	-15
	Right fusiform gyrus		12.40	36	-60	-12
	Left middle occipital gyrus		11.22	-30	-72	27
	Right fusiform gyrus		9.43	42	-36	-27
	Right middle occipital gyrus		9.27	45	-75	0
	Left superior parietal lobule		8.87	-27	-63	45
	Cerebellar vermis		8.01	-3	-72	-27
	Right superior occipital gyrus		7.60	27	-69	30
	Left inferior temporal gyrus		7.48	-60	-54	-15
	Left inferior temporal gyrus	127	8.30	-39	-12	-33
	Left precentral gyrus	118	6.09	-39	9	30
	Left temporal pole	120	5.97	-42	24	-30
	Left medial temporal pole		5.32	-54	12	-30
	Left medial temporal pole		4.66	-30	21	-33
Auditory > visual	Left superior temporal gyrus	4091	11.41	-42	-36	15
	Left superior temporal gyrus		8.81	-51	-21	3
	Left middle temporal gyrus		8.70	-54	-18	0
	Right superior temporal gyrus		8.25	63	-30	9
	Right superior temporal gyrus		7.96	66	-18	3
	Right superior temporal gyrus		7.25	48	-33	21
	Right superior temporal gyrus		7.17	45	-33	15
	Right middle temporal gyrus		6.75	57	-15	-12
	Right cuneus		6.74	12	-72	27
	Left parahippocampal gyrus		6.72	-33	-45	-3
	Right superior temporal gyrus		6.40	63	-12	-6
	Left cuneus		6.38	-9	-72	24

Right precuneus		6.38	9	-54	33
Right precuneus		6.26	12	-51	36
Right superior frontal gyrus	127	5.34	18	45	36
Right superior frontal gyrus		3.93	15	57	27
Left superior orbital gyrus	85	5.26	-9	36	-24
Left superior orbital gyrus		4.24	-9	51	-24
Left ACC	222	5.09	-6	30	-6
Left ACC		4.96	-9	42	-3
Left ACC		4.06	-6	36	6

Table S2. The individual study fMRI parameters.

Study	N	N. Slices	TR	TE	Voxel size	N. volumes
1	14	42	4.15s	70ms	3mm	465
2	15	42	4.07s	70ms	3mm	208
3	20	42	4.07s	75ms	3mm	310
4	20	31	3.2s	70ms	4mm	896