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The contribution of fronto-parietal regions to sentence comprehension: Insights from the Moses illusion

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ABSTRACT

To interpret a sentence, the reader must not only process the linguistic input, but many times has also to draw inferences about what is implicitly stated. In some cases, the generation and integration of inferred information may lead to semantic illusions. In these sentences, subjects fail to detect errors such as in "It was two animals of each kind that Moses took on the ark" despite knowing that the correct answer is Noah, not Moses. The relative inability to notice these errors raises questions about how people establish and integrate inferences and which conditions improve error detection. To unravel the neural processes underlying inference and error detection in language comprehension, we carried out an fMRI study in which participants read sentences containing true or false statements. The false statements either took the form of more obvious (i.e., clearly false) or subtle (i.e., semantic illusions) inconsistent relations. Participants had to decide if each statement was true or false. Processing semantic illusions relative to true and clearly false sentences significantly engaged the right inferior parietal lobule, suggesting higher demands in establishing coherence. Successful versus unsuccessful error detection revealed a network of regions, including right dorsolateral prefrontal cortex, orbitofrontal, insula/putamen and anterior cingulate cortex. Such activation was significantly correlated with overall response accuracy to the illusions. These results suggest that to detect the semantic conflict, people must inhibit the tendency to draw pragmatic inferences. These findings demonstrate that fronto-parietal areas are involved in inference and inhibition processes necessary for establishing semantic coherence.

Introduction

As a sentence or narrative unfolds, the listener builds-up an interpretation of the linguistic input based on various sources of information including semantic, syntactic and pragmatic information. Many times, developing such interpretation involves not just understanding what is said, but also inferring what is implicitly stated. People draw inferences from discourse to establish coherence between individual events (Graesser et al., 1994; McKoon and Ratcliff, 1992). For instance, if one is told that "she no longer writes fiction", one may infer that "she once wrote fiction". A clear example of the role of inference in discourse comprehension is the case of cleft sentences. A cleft sentence divides a proposition into two parts, whereby the cleft constituent expresses the focus and the cleft clause expresses a presupposition (Prince, 1978). In it-cleft sentences such as "It was a poem that he read last night", the focused information ("It was a poem") is typically analyzed exhaustively, whereas the non-focused or background information ("that he read last night") is often assumed to be true and taken for granted (Graesser et al., 1994; McKoon and Ratcliff, 1992). It is well known that focused information is detected more quickly (Birch and Garnsey, 1995; Cutler and Fodor, 1979) and is also better remembered (Singer, 1976) than non-focused information, indicating that focus plays an important role in sentence comprehension.

The extreme case of the effect of focus in cleft sentences is the semantic illusion phenomenon, in which the listener fails to notice a semantic anomaly in a sentence. In the Moses illusion, many participants do not immediately detect errors reading the sentence "It was two animals of each kind that Moses took on the ark" despite later showing knowledge that the correct reference is Noah, not Moses (Erickson and Mattson, 1981). The close semantic relationship between the incorrect word (Moses) and the critical word (Noah) is a prerequisite for the illusion to occur (Barton and Sanford, 1993; Ferreira et al., 2002; Park and Reder, 2004; van Oostendorp and de Mul, 1990). However, the sentence focus crucially affects the illusion rate. In the standard illusion, participants direct their attention to the main focus of the sentence that contains true information ("It was two animals of each kind") and miss the incorrect presupposition ("that Moses took on the ark"), resulting in a high illusion rate (Brédart and Modolo, 1988). In contrast, the illusion significantly decreases when the focus shifts to the inconsistent part of the sentence, such as in "It was Moses who took two animals of each kind on the

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ark". Thus, in the standard Moses illusion, people draw a pragmatic inference that the non-focused information is true, processing this given or background information in a semantically shallow manner (Brédart and Docquier, 1989; Brédart and Modolo, 1988; Sanford et al., 2006). To fully and properly process these cleft sentences, readers must compute this pragmatic inference. More specifically, to detect the anomaly in the sentences, people must monitor and inhibit the automatic inference that the given, non-focused information is correct (Sanford and Sturt, 2002; Sturt et al., 2004).

In this fMRI study, we use the Moses illusion to investigate the neural network involved in establishing coherence and detecting errors in sentence processing. We chose the Moses illusion paradigm because it is a very robust phenomenon, easily obtained in the laboratory and a useful tool for exploring the construction of meaning. By comparing conditions under which people fall prey to the illusion and those in which people are able to correctly detect errors we can disentangle distinct sentence comprehension processes. Not noticing the error indicates that people accept the standard implication that the non-focused information is accurate and build-up a coherent representation of the sentence (Sanford and Sturt, 2002). In contrast, the ability to detect errors presumably requires executive control processes, such as conflict monitoring and response inhibition processes (Bottoms et al., 2010; Hoenig and Scheef, 2009). Thus, we apply this paradigm to investigate the neural mechanisms supporting core aspects of sentence comprehension. More specifically, we aim to identify the brain regions associated with drawing inferences to establish coherence, and to explore which areas are recruited when errors are successfully detected.

Patient data and fMRI studies have provided some insights into the brain regions that support the elaboration of inferences in order to derive a coherent message-level interpretation. Neuropsychological studies have shown that right hemisphere lesions are associated with impaired comprehension of discourse that requires the generation of inferences (e.g., Beeman, 1993; Brownell et al., 1986). For instance, in a study in which participants listened to stories that promoted inferences, Beeman (1993) reported that right hemisphere-damaged patients answered less accurately to inference questions than explicit questions compared to controls and also responded more slowly to inference-related than unrelated words in a lexical decision task. Supporting the neuropsychological literature, fMRI studies that compared coherent and incoherent texts have also implicated the right hemisphere in establishing discourse coherence (Kuperberg et al., 2006; Mason and Just, 2004; Xu et al., 2005). Mason and Just (2004) presented participants with two-sentence passages that varied in their degree of causal relatedness. The results showed that the ability to draw elaborative inferences was mediated by two cortical networks, a reasoning system in bilateral dorsolateral prefrontal cortex associated with the generation of inferences, and a right hemisphere language network linked to the integration of inferences in context. In another fMRI study, Kuperberg et al. (2006) have investigated the neural mechanisms underlying discourse comprehension, and particularly those mediating the establishment of inferences across sentences. The authors found a sustained engagement of right inferior parietal cortex and bilateral temporal–prefrontal cortices when participants had to generate and use inferences to build up coherence across sentences. Taken together, these data suggest that making sense of discourse involves an extensive cortical network including right fronto-parietal areas to understand what is implicitly stated. It has been proposed that this network reflects the activation, retrieval and integration of information from semantic memory into incoming discourse structure during the processing of inferences (Kuperberg et al., 2006).

In contrast, successful error detection involves increased monitoring processes, in order to detect that the sentence contains a semantic anomaly that conflicts with world knowledge (Bottoms et al., 2010). Studies have suggested that monitoring response conflict involves anterior cingulate cortex (ACC) activation (Badre and Wagner, 2004; Braver et al., 2001). It has been proposed that the ACC signals the occurrence of conflict in information processing, thereby triggering compensatory adjustments in cognitive control (Botvinick et al., 2004). Critically, in order to answer accurately to the illusions, people must not only detect the conflict in the sentence, but also to inhibit the tendency to respond that the sentence is correct. Imaging studies investigating inhibitory control in the decision-making literature have highlighted the role of right lateral PFC in response inhibition (Aron et al., 2004; Chikazoe et al., 2007; De Neys et al., 2008; Hoenig and Scheef, 2009). However, in the context of sentence comprehension, it is still unclear whether similar regions would be recruited to overcome a dominant response tendency.

We addressed these issues in an fMRI study that used Moses illusion type sentences and a sentence verification task. Sentences in the study differed in the degree to which information was semantically coherent: sentences were either true (i.e., statements containing correct semantic and world knowledge information, e.g., *It was Batman who swore to revenge his parents' death fighting against crime*); clearly false (i.e., statements that clearly violated world knowledge; *It was the hunters who killed Bambi's mother when she was on the beach*); or semantic illusions (i.e., statements containing a semantic error that was difficult to detect; *It was the terrible stepmother who tried to kill Cinderella with a poisoned apple*). Based on previous behavioral studies (Reder and Kusbit, 1991), we hypothesized that verifying sentences containing semantic illusions is more demanding than verifying both true sentences (where conceptual relations are intact) and false sentences (in which the semantic incongruence is easily detected). In semantic illusions, a focus on the cleft constituent of the sentence ("It was the terrible stepmother") and the overlook of the cleft clause ("who tried to kill Cinderella with a poisoned apple") will lead to the incorrect inference that the sentence is true and to the inappropriate integration of the error in sentence comprehension. Such generation and integration of inferences should be associated with increased response in the right hemisphere regions, namely in the inferior parietal cortex, during processing of illusions compared to other types of sentences (Kuperberg et al., 2006). Moreover, within the semantic illusion condition, successfully noticing the error, relative to failing to notice the error, should involve frontal activation associated with executive control (Hoenig and Scheef, 2009; Rodd et al., 2010). In order to answer correctly to the illusions, people must monitor the conflict in the sentence and additionally must inhibit the intuitive but inappropriate response. Thus, we expect ACC activation linked to conflict monitoring (Botvinick et al., 2004) and right lateral PFC activation associated with response inhibition (De Neys et al., 2008) to be particularly relevant during successful detection of illusions.

Method

Participants

Seventeen right-handed, healthy participants, native speakers of Portuguese (18–25 years old, 16 females) took part in the study. All gave informed written consent to the experimental procedure, which was approved by the local ethics committee.

Materials and procedure

The stimuli consisted of 160 written sentences, half of which were true statements (e.g., *It was Batman who swore to revenge his parents' death fighting against crime*), and half of which were false. Within the false sentences, half were clearly false, i.e., they contained a highly implausible reference (e.g., *It was the hunters who killed Bambi's mother when she was on the beach*), while the other half were semantic illusions, i.e., sentences that contained a plausible but misleading reference (e.g., *It was the terrible stepmother who tried to kill Cinderella with a poisoned apple*). Most semantic illusions were modified from published papers (Bottoms et al., 2010; Brédart and Modolo, 1988; Burke et al., 1991; Buttner, 2007; Erickson and Mattson, 1981; Hannon and Daneman, 2001; Marques, 1991; Park and Reder, 2004; Reder and Kusbit, 1991) and some were originally constructed. Even though both clearly false sentences and semantic illusions contained false information in the non-focused part of the sentence, the anomaly in the latter (*Cinderella*) is much more difficult to detect, since it is very closely related in meaning to the correct critical word (*Snow White*, Van Oostendorp and De Mul, 1990). In contrast, in the clearly false condition the error is semantically distant from the critical word. Therefore, even a shallow semantic processing of the non-focused information is enough to detect the anomaly. The semantic relationship between the anomalous word and the correct critical word in both semantic illusions and clearly false sentences was confirmed in a pretest (Table 1). A group of 20 participants (who did not take part in the fMRI study) rated the erroneous words presented in the semantic illusion condition as significantly more related to the correct answer than the anomalous words in the clearly false condition ($p < .001$).

Each semantic illusion sentence was paired with a clearly false sentence and with two true sentences. As it can be seen in Table 1, sentences in each condition had a similar number of words ($p > .05$), similar structure and theme. All sentences were related to general knowledge information, including geography, politics, cartoons, literature and history. Moreover, the anomalous words in the semantic illusion and clearly false conditions were matched in length and word's position in the sentence, ruling out any word size or word position effects across different conditions ($p > .05$). All materials were in Portuguese.

Each sentence was presented on the screen for 4500 ms during which participants had to decide if the statement was true or false, by pressing the left index finger for true and the left middle finger for false. We included 40 baseline items to control for the visual and motor demands of the task. This corresponded to strings of plus signs (e.g., +++ ++++++ ++ ++++) that appeared for 4500 ms and participants had to press the left index finger for each string. Successive trials were separated by a variable inter-stimulus interval (500, 1000 and 1500 ms in proportion of 4:2:1) in order to optimize statistical efficiency (Dale, 1999).

The items were pseudo-randomly organized into two sessions of 100 trials each (40 true sentences, 20 clearly false sentences, 20 semantic illusion sentences and 20 baseline trials), with session order counterbalanced across participants. Each scanning session started with one-minute rest (i.e., low level baseline), during which subjects saw a blank screen and no response was required. Each session lasted approximately 10 min. Presentation and timing of stimuli were controlled using EPrime software (www.psnet.com). We recorded both reaction times and accuracy during fMRI data acquisition.

Following the completion of the experiment, participants were asked to answer an unexpected questionnaire outside the MR scanner. The goal was to evaluate participants' knowledge about the 40 semantic illusions. For example, participants were required to give an answer to the question "*Who did the terrible stepmother try to kill with a poisoned apple?*". If participants know the correct answer, they should answer "*Snow White*" even though they may have failed to detect the anomaly (*Cinderella*) when presented in the semantic illusion sentence (Erickson and Mattson, 1981).

Table 1
Descriptive statistics of stimuli characteristics.

Sentence type	N	Sentence length (words)	Anomalous word position	Anomalous word length (characters)	Semantic relationship
Illusion	40	12.1 (2.2)	9.0 (3.9)	8.0 (3.3)	5.0 (0.9)
E.g., *It was the terrible stepmother who tried to kill Cinderella with a poisoned apple.*					
False	40	12.2 (2.2)	9.6 (3.4)	8.3 (3.6)	3.5 (0.6)
E.g., *It was the hunters who killed Bambi's mother when she was on the beach.*					
True	80	12.2 (2.2)	–	–	–
E.g., *It was Batman who swore to revenge his parents' death fighting against crime.*					

MRI acquisition and imaging analysis

Scanning was conducted at Sociedade Portuguesa de Ressonância Magnética on a 3-Tesla Philips MR system (Philips Medical Systems, Best, NL) using a standard head coil. Functional data were acquired by using an echo-planar sequence (TR = 2000 ms, 34 interleaved slices parallel to the AC-PC line, with isotropic voxels, 2 mm thick, interslice gap of 1 mm, 2 mm × 2 mm in-plane resolution, FOV = 23 cm × 23 cm, matrix size = 116 × 115). Acquisition covered the entire brain. Before functional data collection, three dummy volumes were discarded to allow for T1 equilibrium. High-resolution T1-weighted anatomical images were acquired for visualization.

Preprocessing and statistical analysis of the data were performed using Statistical Parametric Mapping software (SPM5, Wellcome Institute of Cognitive Neurology, www.fil.ion.ucl.ac.uk), implemented in MATLAB (MathWorks Inc., Sherborn MA, USA). Slice acquisition timing was corrected by resampling all slices in time relative to the middle slice collected, followed by rigid body motion correction across all sessions. Functional data were spatially normalized to a canonical echo-planar imaging template using a 12-parameter affine and nonlinear transformation, and then spatially smoothed with an 8 mm Gaussian kernel. We modeled the responses to each condition (true, false, illusion and control trials) separately.

Participants were treated as random effects. Data for each subject were modeled with the general linear model using the canonical hemodynamic response function (HRF). The least squares parameter estimates of the best-fitting canonical HRF for each condition of interest were used in pairwise contrasts and stored as a separate image for each subject. These images were then tested against the null hypothesis using one-tailed *t* tests. Activations were considered significant if they consisted of twenty or more contiguous resampled voxels (2 mm isotropic) and exceeded an alpha threshold of .001 for simple contrasts (Forman et al., 1995; Lieberman and Cunningham, 2009). Montreal Neurological Institute coordinates are reported. Beta values were obtained for the peak activations. These data were further analyzed using off-line statistical software.

Results

Behavioral data

Separate ANOVAs were conducted on the proportion of correct responses and on response time (RT) data. There was a significant difference in accuracy between illusions and true sentences ($t(118) = -13.0$, $p < .001$), as well as between illusions and clearly false sentences ($t(78) = -9.8$, $p < .001$), showing that participants were significantly more accurate in verifying true and clearly false statements than semantic illusions. There was no significant difference in accuracy between true and clearly false statements ($t(118) = 1.0$, $p > .1$; see Table 2). Regarding RTs, semantic illusions revealed significantly slower responses than both true ($t(118) = 3.5$, $p < .001$) and clearly false sentences ($t(78) = 2.9$, $p = .005$). However, there was no significant difference in RTs between true and clearly false statements ($t(118) = 0.8$, $p > .1$; see Table 2). Within the semantic

Table 2
Mean (and standard deviation) of proportion of correct responses and RT for each sentence condition.

	Accuracy	RT
Illusion	.38 (.19)	3156 (234)
False	.77 (.17)	2983 (295)
True	.81 (.16)	2930 (370)

illusion condition, we found no significant difference in RTs between correct and incorrect responding (mean correct = 3250 ms; mean incorrect = 3116 ms; $t(39) = 1.9$, $p > .05$). The results suggest that semantic illusions involved higher semantic demands than other types of sentences, regardless of whether or not participants noticed the errors.

Of particular interest was whether participants had correct knowledge about the information in the semantic illusion sentences. The post-scan knowledge-check questionnaire showed that participants responded correctly to 78% of the questions, regardless of whether or not they had noticed the error in the sentence in the earlier phase of the study. Considering only the items answered correctly on the knowledge-check questionnaire, we found that in the earlier sentence verification task, participants fell prey for the illusion in 60% of those sentences, while correctly noticing the error in 40% of the sentences. This significant difference ($t(39) = 3.6$, $p = .001$), shows that participants missed most of the incorrect information in the semantic illusion sentences, even though they later demonstrated correct knowledge of the critical facts.

Overall, the results demonstrated that it was significantly more difficult to verify the veracity of information in semantic illusion sentences than in true and clearly false sentences. Moreover, participants failed to notice errors in the illusions even when they later showed correct knowledge about the depicted information.

Functional imaging data

We first investigated the brain regions engaged during processing of written sentences, by comparing all sentences (illusion, true and clearly false) against baseline (series of plus signs). As expected, a mainly left-lateralized distributed network across frontal, temporal and occipital cortices was found, suggesting that this experiment successfully tapped into the semantic processing system.

To determine the neural substrate mediating the generation and integration of inferences, we compared semantic illusions (both correct and incorrect responses) with true sentences. In both conditions, participants may infer that the non-focused, background information is true. However, while for true sentences such inference is adequate, for semantic illusions the integration of the inference in the sentential context may be more demanding as there is an error in the sentence. Processing semantic illusion sentences relative to true sentences engaged the R inferior parietal lobule (IPL, BA 40), posterior cingulate gyrus (BA 23), L putamen (BA 48) and L precentral gyrus (BA 4; Fig. 1, Table 3). The opposite contrast of true sentences (where semantic relations are intact and the given information may be appropriately integrated) relative to illusions did not show any significant activation.

We also compared semantic illusions (both correct and incorrect responses) with clearly false statements. In this contrast, both types of sentences are false, but while for illusions people may attempt to generate and integrate the pragmatic inference, for clearly false sentences such inferential processes should not take place as the error is easily detected. We found significant activation in the R IPL (BA 40) and L precentral gyrus (BA 4), as well as a significant cluster in the R angular gyrus (BA 39) for illusions compared to clearly false sentences (Fig. 2A, Table 3). In contrast, the clearly false condition relative to the semantic illusion condition recruited two regions in the bilateral temporal cortex, namely the R ITG (BA 37) and the L lingual gyrus (BA 19; Fig. 2B, Table 3).

To further explore the processing of semantic illusions, and specifically the relationship between brain activity and the ability to detect the error in these sentences, we carried out a new analysis in which the proportion of correct responses to the illusions was used as a covariate. This whole brain correlation analysis allowed us to examine which brain regions are increasingly recruited for successful versus unsuccessful error detection as behavioral performance improves. In this analysis, correct and incorrect responses to the illusions were modeled separately, and we took into consideration only those items

Table 3
Regions demonstrating increases of response to semantic illusions relative to true sentences, semantic illusions relative to false sentences and false sentences relative to semantic illusions.

Region	BA	No voxels	*Z*-score	MNI coordinates		
				x	y	z
Illusion > True						
L precentral gyrus	4	52	4.19	−32	−20	52
L putamen	48	41	3.83	−22	20	4
Posterior cingulate cortex	23	57	3.72	−4	−28	44
R inferior parietal lobe	40	40	3.49	40	−46	50
Illusion > False						
L precentral gyrus	6	38	4.02	30	−6	40
R inferior parietal lobe	40	24	3.59	52	−40	48
R angular gyrus	39	38	3.51	42	−64	42
False > Illusion						
R inferior temporal gyrus	37	32	3.89	46	−46	−18
L lingual gyrus	19	27	3.75	−32	−86	−12

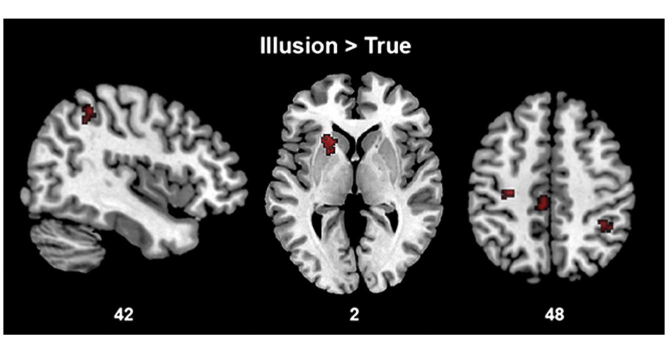

Fig. 1. Cortical regions activated for semantic illusions minus true sentences. Activations were overlaid on a canonical brain and thresholded at $p = .001$, 20 voxels.

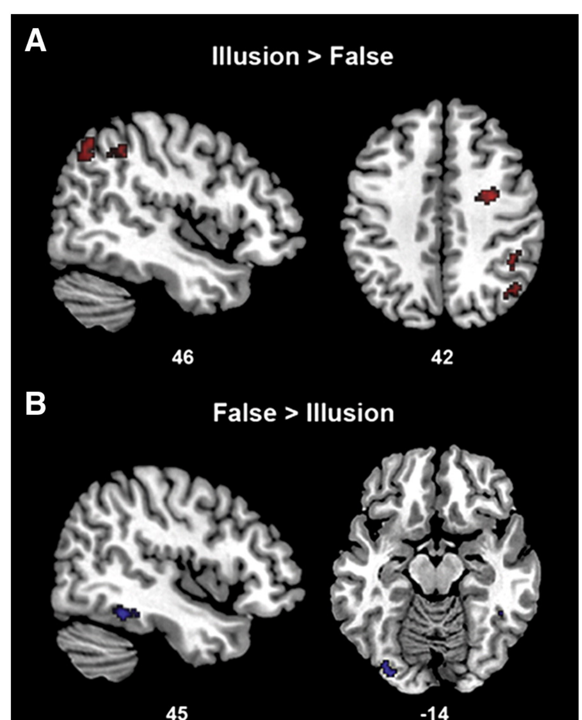

Fig. 2. (A) Cortical regions activated for semantic illusions minus false sentences. (B) Cortical regions activated for false sentences minus semantic illusions. Activations were overlaid on a canonical brain and thresholded at $p = .001$, 20 voxels.

answered correctly on the post-scan questionnaire, since these are the only items that we can assume that the participant knew during the sentence verification task. Illusions for which participants did not respond correctly in the post-scan questionnaire were modeled as a separate condition and were not further examined. This analysis revealed stronger activation in several regions during successful detection of semantic errors as behavioral performance improved ($p < .005$, > 20 voxels). These regions included the R dorsolateral PFC (BA 45), R orbitofrontal cortex (BA 11), R insula/putamen (BA 48), L postcentral gyrus (BA 3) and anterior cingulate (BA 32; Fig. 3, Table 4). Finally, we inspected the signal change in the R dorsolateral PFC (BA 45), a region for which we predicted greater activation during successful than unsuccessful error detection in the semantic illusion condition. As illustrated in Fig. 3B, an increased recruitment of R dorsolateral PFC during successful error detection was associated with an enhanced behavioral performance to the illusions. ($r = .68$; $p < 0.05$). In short, those subjects who showed the largest R dorsolateral PFC responses during successful error detection also showed the greatest response accuracy to the illusions.

In sum, the neuroimaging results showed that processing sentences containing semantic illusions activated regions in the R inferior parietal and precentral gyri, over and above other types of sentences. In addition, correctly detecting errors in these sentences engaged a network of regions, including the R dorsolateral PFC, R orbitofrontal, R insula/putamen and anterior cingulate gyrus. The magnitude of the activation in such regions, namely in the R dorsolateral prefrontal cortex, was correlated with increased response accuracy for semantic illusions.

Table 4
Regions demonstrating a correlation between increases of response to successful relative to unsuccessful error detection and response accuracy in the illusion condition.

Region	BA	No voxels	*Z*-score	MNI coordinates		
				x	y	z
Brain–behavior correlation						
L postcentral gyrus	3	78	4.32	−26	−30	34
L precentral gyrus	48	31	3.44	−36	−8	32
L anterior cingulate gyrus	32	36	3.38	−14	36	34
L occipital gyrus	7	49	3.32	−20	−56	34
R orbitofrontal gyrus	11	39	3.24	16	20	−16
R insula/putamen	48	169	3.22	36	14	−8
R dorsolateral PFC	45	32	3.05	36	40	2

Discussion

The goal of the present study was to investigate the neural processes engaged when people comprehend and judge the coherence of sentences and to elucidate the neural regions involved in the correct detection of semantic anomalies. For this purpose, we used semantic illusion sentences, which pose a high demand on both semantic coherence and error detection, as they contain a semantic anomaly that is difficult to notice.

Sentences containing semantic illusions, compared to both true and clearly false sentences, revealed increased activation in R inferior parietal cortex. The increased involvement of R-lateralized regions is in line with a growing number of studies reporting additional activation in the right hemisphere, especially when semantic or linguistic demands are particularly high (Bozic et al., 2010; Friederici, 2011; Hoenig and Scheef, 2009; Jung-Beeman, 2005; Rodd et al., 2005; Tesink et al., 2011). Bilateral parietal activation, namely in the angular gyrus, has also been reported when understanding the speaker's intended meaning requires increased semantic and pragmatic integration of inferences, as for example in the case of processing humor (Bekinschtein et al., 2011). Moreover, it has been suggested that R inferior parietal cortex activation may reflect processes associated with drawing inferences to establish coherence across the text. In particular, Kuperberg et al. (2006) have proposed that R inferior parietal cortex, along with other bilateral regions, may reflect causal inference across sentences, when participants' attempt to generate and integrate information that is implicitly stated. In the present study, significant activation was observed in this region during the processing of semantic illusions (relative to true and clearly false sentences), suggesting that inference demands are higher for these sentences. Semantic illusions may seem odd or unlikely compared to true statements, but the error is not as easily detected as in the case of clearly false statements, making it harder to arrive at a coherent representation. This interpretation is also consistent with recent ERP studies showing that the Moses illusion affects the P600 amplitude. This effect may be related to an increased effort in establishing a representation of what is being communicated. In particular, it may reflect an effort associated with assigning relations between elements of the sentence and establishing inferences, including pragmatic knowledge about communication (Brouwer et al., 2012; Sanford et al., 2011).

The increased neural response for illusions was accompanied by significantly longer RTs and lower accuracy, confirming that, when deciding if a sentence is coherent or not, semantic illusions yield higher semantic and pragmatic demands than other types of sentences. Even

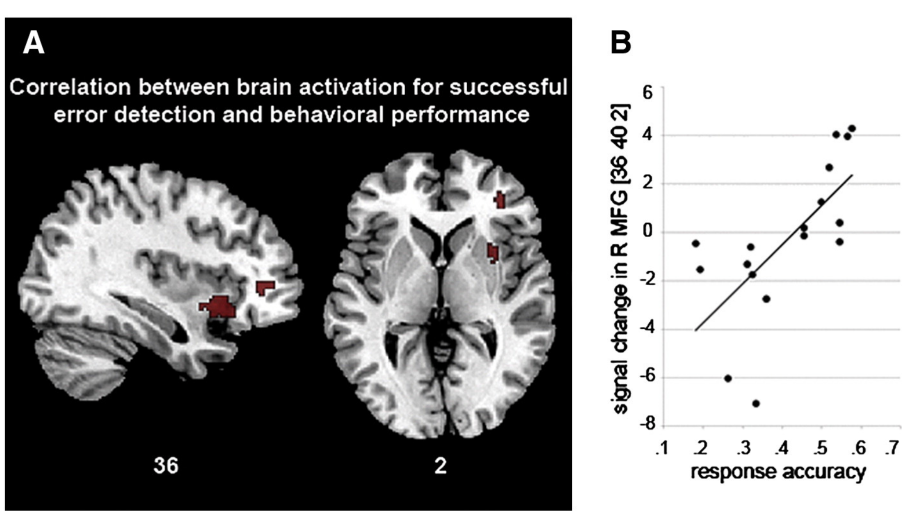

Fig. 3. (A) Cortical regions demonstrating a correlation between increases of response to successful relative to unsuccessful error detection and response accuracy in the illusion condition. Activations were overlaid on a canonical brain and thresholded at $p = .005$, 20 voxels. (B) Correlation between the parameter estimates extracted from the R middle frontal gyrus and behavioral performance in the illusion condition.

when the semantic anomaly is not detected, participants are slower in verifying these sentences than true sentences. It is plausible that participants are to some extent aware of the anomaly, due to bottom-up processes associated with the analysis of the linguistic input (e.g., word by word analysis of the stimulus). These bottom-up processes may be in conflict with more top-down influences, such as pragmatic reasoning, resulting in longer RTs for semantic illusions than other types of sentences (Shafto and MacKay, 2010). It is also important to note that, along with the generation and integration of inferences, establishing coherence involves other cognitive processes. These include activation, retrieval and selection of information within long-term semantic memory, its short-term retention in working memory, and its encoding into long-term memory (Kuperberg et al., 2006). Specifically, differences in retrieval between illusions and true sentences may arise, since the correct critical word (e.g., Noah) is more strongly predicted or primed than the incorrect word (e.g., Moses). Indeed, some studies have suggested that inference generation involves the automatic activation of semantic associations, which may occur through priming of specific words in a constrained discourse context (McKoon and Ratcliff, 1989). Moreover, working memory demands may also have been particularly high for processing illusions as the activated semantic information had to be held online to perform the coherence judgment task. It is therefore possible that the increased RTs for semantic illusions was driven, in part, by the increased working memory load associated with establishing coherence in these sentences (Hannon and Daneman, 2001; Singer and Ritchot, 1996). Our study was not designed to disentangle between these alternative explanations, but an interesting goal for future research involves a finer grained analysis of the several processes engaged in establishing semantic coherence.

In contrast to the illusions, clearly false sentences were associated with activation in bilateral middle and inferior temporal regions when compared to semantic illusion sentences. Like semantic illusions, false sentences also contain a semantic anomaly but in this case, the error is easily detected, and therefore the integration of the erroneous word in the sentence will not be carried out. Response in these temporal regions may be associated with the automatic reactivation of lexical–semantic representations when the meaning of the sentence must be reinterpreted, after the reader encounters a semantic error (Kuperberg et al., 2008; Rodd et al., 2012). This reactivation may also reflect increased top-down demands associated with the retrieval of world knowledge or knowledge about the likelihood of an upcoming word, during the processing anomalous or uninterpretable sentences (Davis and Rodd, 2011; Rodd et al., 2012).

We probed the neural network involved in the detection of semantic errors looking at the correlation between brain activity associated with successfully detecting the anomaly (versus not noticing the error) and the behavioral accuracy in the semantic illusion condition. Since this analysis included only the sentences for which participants had correct knowledge (as revealed by the post-scan questionnaire), any differences between conditions and participants cannot be attributed to the level of familiarity or experience with the sentences' content. This analysis yielded a significant activation in a set of regions, including the R dorsolateral PFC, R orbitofrontal cortex, R insula/putamen and ACC. The tendency to recruit this network during error detection correlated with differences in response accuracy, such that greater engagement of these regions was associated with better performance in the illusion condition (as illustrated in Fig. 3). These regions play an important role in conflict monitoring and response inhibition. For example, in a study using three response inhibition tasks (a go/no-go task, a flanker task and a stimulus-response compatibility task), Wager et al. (2005) found several commonly activated regions, namely R dorsolateral PFC, bilateral insula and ACC. Interestingly, activation in this network tracked behavioral performance in each task, suggesting that the network is sensitive to the amount of interference encountered by the participants. Moreover, a recent meta-analysis of go/no-go tasks demonstrated a primarily right-lateralized network associated with successful inhibition, including R prefrontal, bilateral putamen and insula, bilateral occipital areas and supplementary motor area bordering the ACC (Simmonds et al., 2008).

Research in the reasoning and decision-making literature have reported R lateral PFC recruitment during the inhibition of an intuitive response that conflicts with probabilistic or logical reasoning (De Martino et al., 2006; Prado and Noveck, 2007). In these tasks, people must detect the conflict between intuition and probability and subsequently inhibit the intuitive response in order to answer correctly. Similarly, a recent fMRI study showed that a similar region of the R inferior frontal gyrus was involved in the processing of false counterfactual sentences (Nieuwland, 2012). The authors argued that this region might play an important role in inhibitory control, namely inhibiting competing concepts in order to detect the adequate concept for message-level integration. Along the same line, in the current study, in order to identify the false status of a semantic illusion, participants must suppress the fairly automatic pragmatic inference. The inhibition of inferences will facilitate the detection of the semantic conflict between the critical word and the rest of the sentence, and subsequently prevent the tendency to respond that the sentence is correct. Thus, semantic illusions may induce a dominant but inappropriate response that must be inhibited via a network of right frontal areas, namely R dorsolateral PFC, ACC, R orbitofrontal and R insula/putamen. As expected, activation in the R dorsolateral PFC increased when participants successfully detected the semantic errors and responded correctly to the illusions. Participants differed in the degree to which they recruited R dorsolateral PFC during successful relative to unsuccessful error detection. Importantly, these differences tracked the subjects' ability to perform the task.

Interestingly, some of these regions, namely the R orbitofrontal gyrus and R insula/putamen, have also been implicated in the processing emotion and reward (Clark et al., 2009; Delgado et al., 2000) and have been reported during rejection of false sentences (Harris et al., 2008). Since our paradigm did not use any explicit reward or feedback, we propose that recognizing the subtle error in the semantic illusions may be in itself rewarding for the subject, as it fulfills the subject's a priori goals.

In summary, our results demonstrate the critical role of fronto-parietal areas in establishing a coherent representation of sentences. Within this network, activation of R inferior parietal lobule was modulated by the demands in generating and integrating inferences. We suggest that activity in R dorsolateral prefrontal cortex, along with ACC, R orbitofrontal and R insula/putamen, reflects processes that are required to detect subtle semantic contradictions, namely conflict monitoring and the inhibition of pragmatic inferences.

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Conflict of interest statement

There is no conflict of interest.

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