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How metaphors influence semantic relatedness judgments: The role of the right frontal cortex

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We used event-related fMRI (ER-fMRI) to test the hypothesis that metaphors bias cognitive processing of semantic relatedness towards a search for a wider range of associations. Twelve right-handed male volunteers read a mixture of metaphoric and literal sentences, each sentence being followed by a single word, which could be semantically related or not to the preceding sentence context. We found that judging unrelated words as contextually irrelevant was associated with increased blood oxygenation level-dependent (BOLD) signal in the right ventrolateral prefrontal cortex in the metaphoric but not in the literal condition. The same region was also activated when subjects endorsed a semantic relation between words and metaphoric sentence primes but not between words and literal sentence primes. We argue that these results are consistent with the notion of semantic open-endedness, whereby figurative statements bias cognitive processing towards a search for a wider range of semantic relationships compared to literal statements, and thus lend further support to the view that coarse semantic coding occurs preferentially in the right hemisphere.

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Introduction

What does it take to decide whether or not the meanings of two linguistic variables are related? Do metaphors evoke a wider range of semantic associations, and which brain resources are required to affirm or discard a semantic connection between linguistic items? In recent years, there has been an intensive research effort to combine up-to-date neuroscience methodology with empirical data from psycholinguistics in order to describe the neural networks involved in semantic processes (Gernsbacher and Kaschak, 2003; Stowe et al., 2005), which might answer these questions. The

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¹ These authors contributed equally to the accomplishment of this work. Available online on ScienceDirect (www.sciencedirect.com). theoretical grounds from which such work emerges is often derived from linguistics. The focus ranges from sentence semantics, e.g., the distinct brain mechanisms involved in understanding figurative compared to literal statements (Ahrens et al., in press; Rapp et al., 2004; Stringaris et al., in press), to exploring the differential hemispheric processing of salient versus non-salient items (Giora et al., 2000; Mashal et al., 2005 in press), and the importance of contextual clues in comprehending sentence information (Xu et al., 2005).

Figurative statements, such as metaphors and idioms, typically contain a meaning which differs from their literal interpretation. Such statements are prevalent in everyday communication (Gibbs, 1994; Glucksberg, 2003) and are also pervasive across a wide range of human discourse, utilized in describing scientific theories (Boyd, 1993) and in shaping political discussions regarding scientific discoveries (Nelkin, 2001). Furthermore, clinical evidence suggests that figurative language may be differentially impaired in certain psychiatric and neurological disorders, such as schizophrenia (Chapman, 1960; Cutting and Murphy, 1990; Sponheim et al., 2003), Alzheimer's dementia (Papagno et al., 2003), and traumatic brain injury (Dennis and Barnes, 1990). Interest in figurative language in general and in metaphor research in particular has been further spurred by considerable advances from the field of psycholinguistics. Solid empirical data emerging over the last two decades (Gibbs, 1994; Glucksberg et al., 1982; Glucksberg, 2003) challenge the classical view attributed to Aristotle (Aristotle, 1952) and later supported by Grice (1975) and Searle (1993), which posits that upon reading a sentence, the first attempt is at deriving a literal meaning, and only when this is found to be defective will alternative, non-literal interpretations be considered. Hence, according to Glucksberg and Keysar's (1993) model, a metaphoric statement such as "My job is a jail" would be accessible not via the route of first having to reject the literal meaning as false, but rather through a more or less direct category comparison in which the connection between job and jail is made on the basis of both belonging to the common attributive category of unpleasant and confining situations.

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Against this background, recent studies have used neuroimaging in an attempt to shed light on the brain mechanisms underlying metaphor comprehension. Perhaps the most striking finding of these studies is the convergence of evidence regarding the role of the left frontal cortex in processing metaphors. For instance, using event-related fMRI (ER-fMRI), Rapp and colleagues (2004) found that, compared to literal sentences, reading metaphors led to activations in the left inferior frontal (BA 45/47) and the left temporal cortex. Similarly, a further fMRI study (Stringaris et al., in press) also found increased blood oxygenation level-dependent (BOLD) responses in the left inferior frontal gyrus (BA 47) as well as in the left thalamus. A block design fMRI study (Lee and Dapretto, 2006) also showed increased activation in the left inferior frontal cortex (BA 44/45). These findings have cast doubt on the more traditional view that figurative meanings are preferentially processed in the right hemisphere (RH), which was itself based on lesion studies (Brownell et al., 1990; Winner and Gardner, 1977) and a PET experiment (Bottini et al., 1994). Instead, a consensus seems to emerge suggesting that it is increased complexity or relative low salience of linguistic items rather than metaphoricity per se that predicts involvement of the RH (Giora, 2006).

The notion that aspects such as the familiarity of linguistic items and their interpretation may primarily determine their neural representation is reflected in the graded salience hypothesis (GSH) (Giora, 1999, 2003). According to the graded salience hypothesis, meanings coded in the mental lexicon, enjoying cognitive prominence due to, e.g., experiential familiarity, frequency, conventionality, or prototypicality, are salient and will be accessed automatically, regardless of context and figurativity. Coded meanings, low on these variables, are less salient and will be accessed more slowly. Non-coded, novel interpretations might activate salient meanings initially and novel interpretations subsequently. Although more salient meanings are processed in the LH, less, and non-salient interpretations, involving creating distant or less salient semantic relations, will be processed in the RH (Giora et al., 2000; Jung-Beeman, 2005). Recent neuroimaging studies have lent considerable empirical support to the GSH. Mashal and her colleagues (in press) compared literal, conventional metaphoric, novel metaphoric, and unrelated word pairs using block-design fMRI. In their study, direct comparisons between novel and conventional metaphoric expressions revealed that the non-salient novel items (inducing non-coded responses) led to significantly stronger activation in the right posteriorsuperior temporal gyrus and the right frontal cortex. This was corroborated by a further study (Mashal et al., 2005a) applying principal components analysis (PCA) to fMRI data which demonstrated a neural network involving right Wernicke's area in the processing of novel but not of conventional metaphoric expressions. These findings received further support by eventrelated potential studies revealing that regardless of sentence type, i.e., literality or metaphoricity, the degree to which the RH will be activated is a function of the remoteness of the semantic relationship between given stimuli (Schmidt et al., in press). Therefore, it seems that the contribution of the right hemisphere increases too as semantic complexity is increased (Jung-Beeman, 2005). Characteristically, searching for contextual relevance of linguistic items leads to activation in the RH (Caplan and Dapretto, 2001; Kircher et al., 2001). Indeed, Xu and colleagues (2005) have recently demonstrated an increase in RH activation as the requirements to resolve contextual complexity increased. It thus looks as if the role of the RH becomes more apparent when experimental conditions approximate aspects of natural language.

In the present study, we sought to investigate a crucial aspect of everyday human communication, namely, how people make judgements on semantic relations. In particular, we were interested in finding out how judging the extent of relatedness of linguistic items is influenced by metaphoricity. Consistent with our previous findings (Stringaris et al., in press), the main hypothesis of this study posits a qualitative difference between figurative and literal statements. This difference is based on the assumption that metaphors are more open-ended in that they evoke a wider network of semantic associations even in situations of functional equivalence at the behavioral level, i.e., when reaction times to stimuli do not differ between the two conditions. The view that metaphors, or more generally, figurative statements, are characteristically open-ended at the semantic level has been long standing (Black, 1993; Boyd, 1993). Surprisingly though, it has not been empirically scrutinized. However, indirect evidence from studies on idioms suggests that even highly salient figurative items evoke a wider range of entailments than their literal counterparts (Gibbs, 1992).

To test this hypothesis, we have designed a novel cognitive task which we combined with ER-fMRI. This involved the presentation of a sentence followed by a single word. The sentence was either literal or metaphoric and the probe word following that sentence context could either be semantically related or unrelated to the sentence meaning. Participants were asked to endorse those words they deemed as bearing a semantic relationship to the sentence context and reject those they deemed irrelevant. They did this by pressing a yes or no button. In essence, this task requires subjects to make explicit semantic judgments about a word in relation to a given sentence context.

In our attempt to demonstrate the effects of metaphorical openendedness on judgments of semantic relatedness, we focused specifically on subjects' brain activity while they engaged in deciding about probes *not* related to sentences' meanings, that is, on the rejection side of the task. This is advantageous as it rules out aha! effects (successfully arriving at a particular meaning) that may confound brain activation patterns (Jung-Beeman et al., 2004; Luo et al., 2004a). Also, each probe word that subjects had to reject following a sentence context was identical between the metaphoric and literal condition; this ensured uniformity across the two conditions. Hence, the experiment was designed in such a way as to give priority to the rejection side of the task, the endorsement part functioning mainly as a control task.

Our main prediction was that although a search for relatedness would be a feature of both the metaphoric and literal condition when a semantic relation was finally endorsed, only metaphors would induce a wide search for semantic relatedness while deciding to reject a word as unrelated. In other words, we expected that in the process of deciding to reject a probe as unrelated, the search for semantic relationships in the literal condition would be more constrained compared to the metaphoric condition, where subjects would attempt to activate remote and less salient meanings in order to account for a potential relationship. Hence, the rejection but not the endorsement side of our task would discriminate between the effects metaphors and literals have on judging semantic relationships.

Based on these theoretical considerations, we predicted that in the process of rejecting a semantic relationship, the metaphoric sentences, on account of their open-endedness, would involve a wider semantic network based on neural substrates distinguishable from their literal counterparts; this would be evident even if behavioral data, i.e., response times, did not show a significant difference between the two conditions. As would be predicted by the coarse semantic coding theory (Jung-Beeman, 2005), we expected that the need to activate more remote and less salient semantic relationships would be reflected by increased right hemispheric activation for the metaphoric compared to the literal condition in the rejection side of the task.

In sum, we predicted that, in the metaphoric but not in the literal condition, rejection would involve accessing and choosing between a wide range of competing semantic concepts and would therefore give rise to activations in right frontal cortical areas, already implicated in processing less salient semantic relationships (Mashal et al., in press; Robertson et al., 2000; Seger et al., 2000).

Methods

Participants

The participants were 12 self-designated right-handed male volunteers with no history of psychiatric or neurological illnesses who were native speakers of English.² They provided written informed consent in accordance with procedures laid down by the local research ethics committee. Mean age was 32.5 years (SD 8.6 years) and mean verbal IQ was 115 (SD 7), as assessed using the National Adult Reading Test (Nelson and Wilson, 1982).

Experimental stimuli and design of the task

As described in a previous study of ours (Stringaris et al., in press), literal (LIT) and metaphoric (MET) sentences of the form "some X are Y" were constructed. The stem of the sentence "Some X are..." was identical across the two categories, with the last word varying between metaphoric and literal meaning. For example, a sentence stem such "Some surgeons are..." would be followed by "fathers" for the LIT, and "butchers" for the MET. These last words were matched to within one letter for length and also to within one standard deviation for the following psycholinguistic norms using the MRC Psycholinguistic database (http://www.psy.uwa.edu.au/ mrcdatabase/uwa_mrc.htm): imageability, and familiarity ratings ((for familiarity (Fam): FamMET mean=531, SD=47.8; FamLIT mean=545.9, SD=44.1; p=0.259; 95% CI lower 41.04, upper 11.28); for imageability (Imag): ImagMET mean = 536.8, SD = 71.9; ImagLIT mean=527.3, SD=68.1; p=0.633, 95% CI lower 30, upper 49). The initial corpus of sentences consisted of 100 pairs, which, following assessment of their comprehensibility, was reduced to 25 sentences which were used for the fMRI version. Construction of metaphoric sentences was based on expressions commonly used in English.

Sentences of either category, literal or metaphoric, were presented one at a time for a fixed duration of 1000 ms and then a single word appeared on the screen underneath the sentence for a duration of 1600 ms. Altogether, the sentence and word were displayed for 2600 ms. This single word was either semantically irrelevant or a word evoking a concept similar to the one described in the sentence and thus semantically relevant.

This design gives rise to four different conditions: literal sentences followed by semantically irrelevant words (IRL, see 1a), literal sentences followed by semantically relevant words (RL, see 2a), metaphoric sentences followed by semantically irrelevant words (IRM see 1b), and metaphoric sentences followed by semantically relevant words (RM, see 2b).

(Sentence contexts)—(probes)

- (1) a. Some answers are emotional—meetings.
 - b. Some answers are straight-meetings.
- (2) a. Some answers are emotional—passion.b. Some answers are straight—honesty.

Sentences of either category were presented according to a "true" random sequence of numbers generated from a random number service (www.random.org). We have ascertained that sentences from any of the four categories were not overrepresented at the beginning or the end of the task by correlating the four experimental conditions with the presentation number of the stimuli (r=0.103, p=0.307; Lawrence et al., 2006). Intervals between stimuli were variable following a Poisson distribution around an average interstimulus interval of 7 s. This "jitter" was introduced in order to increase trial variance and avoid concealment of signal information due to overlap of the hemodynamic response in ER-fMRI experiments (Donaldson and Buckner, 2001; Surguladze et al., 2003). During the interstimulus intervals, a fixation cross was present on the screen, which served as a baseline condition for the hemodynamic response (please refer to the Image acquisition section for details of percentage BOLD-blood oxygenation level-dependent signal change calculations).

Experimental procedure

Subjects were given instructions prior to performing the test. They were asked to read each presented sentence and the word that followed it silently and decide as fast and as accurately as possible whether the meaning of the word was related or not to the meaning of the sentence that preceded it by pressing one of two buttons. They were advised that all sentences were correct and meaningful in either a formal or colloquial way and were given illustrative examples of sentences not included in the study proper. Sentences were presented to the subjects through a standard mirror system and legibility of the items was ascertained prior to commencement of the task; the button box was placed in the subjects' right hand.

Analysis of behavioral data

Only "correct" responses, i.e., responses that coincided with the experimenters' judgement, were included in the analysis. Behavioral data from each subject were averaged across each condition following logarithmic transformation to deal with reaction time outliers (Ratcliff, 1993). Results across the two conditions were compared using paired t tests analyzed using SPSS (SPSS version 12.0.1 for Windows) a t test for independent samples.

² In order to avoid any potential confounding effects related to genderspecific language processing differences, this study was confined to male subjects. Although there is no compelling evidence from behavioral studies to suggest that metaphor comprehension differs between male and female subjects, future functional imaging studies would be useful to address this issue.

Image acquisition

As described previously (Stringaris et al., in press), gradient echo echoplanar imaging (EPI) data were acquired on a GE Signa 1.5 T system (General Electric, Milwaukee WI, USA). A quadrature birdcage headcoil was used for RF transmission and reception. One hundred T2*-weighted images depicting blood oxygenation level-dependent (BOLD) contrast (Ogawa et al., 1990) were acquired over the entire duration of the task at each of 22 near-axial non-contiguous 5 mm thick planes parallel to the intercommissural (AC-PC) line: TE 40 ms, TR 2 s, in-plane resolution 5 mm, interslice gap 0.5 mm. This EPI data set provided almost complete brain coverage. An inversion recovery EPI data set was also acquired. This was a 43 near-axial slice image; with 3mm slices and 0.3-mm slice skip parallel to the AC-PC (TE 80 ms, TI 180 ms, TR 16 s, in-plane resolution 1.5 mm). This highresolution inversion recovery EPI gives excellent soft tissue to CSF contrast for a template image onto which the lower resolution functional data were mapped. The IR-EPI template has the same band width as the low-resolution functional scans to avoid any mismatching of functional to anatomical data as they both have the same inherent geometric distortion.

Individual brain activation maps

Data were analyzed with software developed at the Institute of Psychiatry, King's College London, using a non-parametric approach. Data were first processed (Bullmore et al., 1999a) to minimize motion-related artefacts. A 3D volume consisting of the average intensity at each voxel over the whole experiment was calculated and used as a template. The 3D image volume at each time point was then realigned to this template by computing the combination of rotations (around the x, y, and z axes) and translations (in x, y, and z) that maximized the correlation between the image intensities of the volume in question and the template. Following realignment, data were then smoothed using a Gaussian filter (FWHM 7.2 mm) to improve the signal to noise characteristics of the images.

Responses to the experimental paradigms were then detected by first convolving each component of the experimental design with each of two gamma variate functions (peak responses at 4 and 8 s, respectively). The best fit between the weighted sum of these convolutions and the time series at each voxel was computed using the constrained BOLD effect model suggested by Friman et al. (2003). This reduces the possibility of the model fitting procedure giving rise to mathematically plausible but physiologically implausible results. Following computation of the model fit, a goodness of fit statistic was computed. This consisted of the ratio of the sum of squares of deviations from the mean image intensity (over the whole time series) due to the model to the sum of squares of deviations due to the residuals (SSQratio). This statistic is used to overcome the problem inherent in the use of the F (variance ratio) statistic that the residual degrees of freedom are often unknown in fMRI time series due to the presence of colored noise in the signal. Following computation of the observed SSQratio at each voxel, the data are permuted by the wavelet-based method described and extensively characterized in Bullmore et al. (2001). Repeated application of this method at each voxel followed by recomputation of the SSQratio from the permuted data allows (by combination of results over all intracerebral voxels) the data-driven calculation of the null distribution of SSQratios under the assumption of no experimentally determined response. Using this distribution, it is possible to calculate the critical value of SSQratio needed to threshold the maps at any desired type I error rate. The detection of activated voxels is extended from voxel to cluster level using the method described in detail by Bullmore et al. (1999b). In addition to the SSQratio, the size of the BOLD response to each experimental condition is computed for each individual at each voxel as a percentage of the mean resting image intensity level.

Group maps

The observed and permuted SSOratio maps for each individual, as well as the BOLD effect size maps are transformed into the standard space of Talairach and Tournoux (1988) using the two stage warping procedure described in detail in Brammer et al. (1997). This involves first computing the average image intensity map for each individual over the course of the experiment. The transformations required to map this image to the structural scan for each individual in the first instance and then from structural space to the Talairach template are subsequently computed by maximizing the correlation between the images at each stage. The SSQratio and BOLD effect size maps are then transformed into Talairach space, using these transformations. Group activation maps are then computed by determining the median SSQratio at each voxel (over all individuals) in the observed and permuted data maps (medians are used to minimize outlier effects). The distribution of median SSOratios over all intracerebral voxels from the permuted data is then used to derive the null distribution of SSQratios and this can be thresholded to produce group activation maps at any desired voxel or cluster-level type I error rate. Cluster level maps are thresholded at <1 expected type I error cluster per brain. The computation of a standardized measure of effect SSQratio at the individual level, followed by analysis of the median SSQratio maps over all individuals treats intra and inter subject variations in effect separately, constituting a mixed effect approach to the analysis, which is deemed desirable in fMRI. The SSQ ratios between different conditions represent the sums of squares due to the fitted models for the two conditions divided by the residual sum of squares. The SSQ ratios for this contrast computed from the observed and permuted data for each subject are the mapped onto Talairach space and tested for significance at group level as described above.

Sensitivity of detection of fMRI responses

In order to assess the ability of the above analysis software to detect activations, an extension of the technique described in a previous study (Desco et al., 2001) was used. This involved embedding artificial activations in resting state fMRI data. Artificial fMRI responses were produced using the Balloon model described by Buxton et al. (1998) in the region of the hippocampus (bilateral), extrastriate visual cortex (bilateral), left inferior frontal cortex, and anterior cingulate gyrus. The decision to embed activations using a physiological model and analyze using a pair of gamma variate functions was taken in order to bias detection excessively by using the same method for embedding and analysis. Combinations of gamma functions are commonly used to model BOLD effects in fMRI analysis. The activation sizes simulated (spatial extents) were comparable with those commonly detected in these regions in fMRI experiments on encoding recall, motion perception, and verbal fluency (500-1000 mm³). BOLD effect

sizes of up to 1% were simulated with randomized event-related designs with 10 or 50 events per experiment.

Activations were embedded in the raw fMRI data for 6 subjects with reference to the available anatomy of the images and data were then processed through the individual and group analysis steps described above. The threshold for detection of responses for all designs occurred with a BOLD effect of 0.1-0.15%. With a 1% effect size, approximately 70% of the embedded network was detected with 50 trials and 50% with 10 trials in the event-related simulations. At an effect size of 0.5%, these figures fell to 40% (50 events) and 20% (10 events).

Results

Behavioral results and discussion

As shown in Table 1, response times to semantically irrelevant words following metaphoric (IRM) and literal (IRL) sentences did not show a statistically significant difference (p=0.872, two-tailed paired t test). However, response times to semantically relevant words following metaphoric (RM) sentences were significantly longer than to literal (RL) sentences (p=0.001, two-tailed paired t test). In addition, there was no statistically significant difference between errors made by subjects when judging irrelevant words (i.e., when erroneously endorsing a semantically unrelated word) between the two categories IRL and IRM (mean=1.48, SD=1.09, and mean=1.58, SD=1.62, respectively; p=0.754, two-tailed t test). The absolute numbers of events excluded because they were erroneous replies were, out of a total number of 300 stimuli for each condition, 16(5.3%) for the literal and 19(6.3%) for the metaphoric. Conversely, the difference was significant between the literal and metaphoric categories (RL and RM, respectively) when judging relevant words (i.e., when erroneously rejecting a semantically related word: mean=1, SD=1.18 and mean=4.4, SD=2.31; p=0.001, two-tailed t test).

Behavioral data thus suggest that literal and metaphoric statements differ in how they affect relatedness judgments only when it comes to endorsing a word as related. However, when participants had to reject, that is, to judge a word as unrelated to prior target, their error rate as well as their response times were unaffected by the type of context: it took subjects similarly long to say "no" following both a metaphoric and a literal sentence. Given that our study was specifically designed to assess the effect of prior context on the decision to reject a word as unrelated to prior target, it is important to note that, in terms of behavioral data, no effect of metaphoricity was found.

fMRI results and discussion

Rejecting irrelevant meanings

As shown in Table 2 and Fig. 1, rejecting semantically unrelated probes following a metaphoric sentence led to activation in the ventrolateral cortex (BA 47) in the RH as compared to rejecting semantically unrelated words following a literal sentence (IRM>IRL). In addition, rejecting semantically unrelated probes following a metaphoric sentence led to activations in the left cerebellum and the left inferior parietal lobule.

Conversely, when subjects had to discard the same semantically unrelated words following a literal sentence, activations were observed in the left precuneus, the paracentral lobule, the left angular gyrus, the left inferior parietal lobe, the right temporooccipital-parietal junction, the primary visual cortex bilaterally, and the right thalamus.

Activations obtained from the comparisons between conditions were due to differential activation rather than to deactivation, as evidenced by comparison of each condition with baseline activity (data not shown).

Endorsing relevant meanings

As shown in Table 2 and Fig. 1, endorsing a word preceded by a metaphoric sentence led to activations in the right ventrolateral prefrontal cortex (BA 47), as well as the left cerebellum and the left precentral gyrus, as shown for rejection.

However, approving of the semantic relation of a word to a literal sentence led to activation in the right medial aspect of the inferior frontal cortex (x 43.3, y 29.63, z -7.15), in the left cerebellum, the primary visual cortex, and the left precentral gyrus.

Contrasting the behavioral findings, fMRI results show that judging a probe as semantically unrelated to a prior sentence context is affected by metaphoricity. Thus, rejection of a word following a metaphoric target activated the ventrolateral prefrontal cortex in the RH; however, rejection of a word following a literal sentence did not. Notably, this selective lateralization in favor of the metaphoric condition was observed even when data were analyzed using a more lenient cluster activation threshold (p < 0.01; data available on request). Differences were also found for endorsement of a word. Judging a probe as semantically related to a prior metaphoric sentence activated the right ventrolateral prefrontal cortex. However, endorsing a word following a literal target activated the right inferior frontal cortex. Our findings thus suggest that relatedness judgments are affected by the type of a given sentence context and involve distinct brain activations for words following literals and metaphors. However, a note of caution

Table 1

	Conditions	N	Mean (log)	SD (log)	Mean (ms)	SD (ms)	t	df	Significance (two tailed)	95% CI
(a)										
RT	RL	12	2.9438857	0.11854974	928.6	259.07	-4.494	11	0.001	Lower -0.084126
	RM	12	3.0003535	0.12171278	1078.4	289				Upper -0.028809
(b)										
RT	IRL	12	2.9920612	0.11108372	1046.7	259.7	-0.165	11	0.872	Lower -0.12193
	IRM	12	2.9910755	0.11133024	1046.9	266.2				Upper 0.01416

(a) Descriptive statistics for the reaction times (RT) of literal and metaphoric sentences followed by a semantically relevant word (RL/RM) and the respective *t* test results. Reaction times are presented in milliseconds (ms) and also following logarithmic transformation (log); the latter were used for the *t* statistics.
(b) Descriptive statistics for the reaction times (RT) of literal and metaphoric sentences followed by a semantically irrelevant word (IRL/IRM) and the respective *t* test results. Reaction times are presented in milliseconds (ms) and also following logarithmic transformation (log); the latter were used for the *t* statistics.

Table 2

Activations obtained for contrasts; IRL/IRM denote non-relevant words following a literal or metaphoric sentence, respectively, whereas RL/RM stand for related word following a literal or metaphoric sentence, respectively

p value	Cluster size	Tal (x)	Tal (y)	Tal (z)	BA	Side	Cerebral region
IRL > II	RM						
0.0002	18	-25	-78	15	18	L	Primary visual (peristriate) cortex (V2, V3)
0.002	13	22	-22	9	28	R	Right thalamus
0.0002	15	47	-59	-7	37	L	Inferior post temporal lobe
0.001	10	29	-70	26	18	R	Primary visual (peristriate) cortex (V2, V3)
0.0004	6	-32	-56	37	39	L	Angular gyrus
0.0004	15	-11	-59	42	7	L	Precuneus (parietal association cortex)
0.0002	33	0.00	-37	48	31		Paracentral lobule/ precuneus
0.001	13	-29	-30	48	23	L	Inferior parietal lobe
IRM>1	RL						
0.002	8	-29	-48	-29	71	L	Cerebellum
0.0002	21	-11	-70	-18	71	L	Cerebellum
0.001	18	36	26	-7	47	R	Ventrolateral prefrontal cortex
0.001	11	-32	-52	42	40	L	Precuneus/inferior parietal lobule
RL > RI	М						
0.0004	11	51	-4	-29	20	R	Inferior temporal gyrus
0.0008	7	40	-67	-7	19	R	Fusiform gyrus
0.0002	22	29	26	-2	47	R	Inferior frontal gyrus
0.0002	21	-51	-11	26	Φεβ-00	L	Postcentral gyrus
RM > R	L						
0.0002	54	-3.6	-48	-35	71	L	Cerebellum
0.0007	14	-32	-74	-7	18	L	Primary visual (peristriate) cortex (V2, V3)
0.001	16	43	30	-7	47	R	Ventrolateral prefrontal cortex
0.0002	16	-40	4	37	72	L	Precentral gyrus

The *p* value, voxel size, Talairach coordinates (Tal), Brodmann areas, laterality (Side), and cerebral location are given for each activation. Activations listed here were obtained at a voxel level of p < 0.05 and cluster level of p < 0.025.

is warranted at this point because the observed differences in brain activation may be, at least in part, a consequence of varying levels of cognitive demand incurred by the two conditions; the significant difference in reaction times between literal and metaphoric sentences when endorsing semantic relationships could be seen as pointing to this direction.

Importantly, however, rejection of words as unrelated to metaphoric sentences proved to be an activity highly similar to endorsing a word in this condition. Thus, following a metaphoric statement, both endorsing a word as related and judging it as unrelated involved the ventrolateral prefrontal cortex. Indeed, when activations obtained for rejecting a word following a metaphoric sentence (IRM) were contrasted to activations obtained by endorsing a word following metaphoric sentence (RM), no reliable activity was observed in the right ventrolateral prefrontal cortex, or any other area to distinguish between the two conditions (data not shown). Note that Mashal and Faust (in preparation) also found that a rejection and an endorsement task following novel metaphors activated similar brain regions in the RH. This was not found for the literal targets, where rejection and endorsement of words in terms of relatedness induced activity in different brain areas. Consistent with this finding, when activations obtained by rejecting a word following a literal sentence (IRL) were contrasted to activations obtained by endorsing a word following a literal sentence (RL), the ventrolateral prefrontal cortex showed statistically significant activation in the RL>IRL contrast. Metaphors, then, are different from literals not just in how they affect rejection and endorsement of probes but importantly in how they involve similar neural substrates when search for relatedness is induced, regardless of task.

It should be noted that additional activations of the left inferior frontal gyrus and left temporal cortex where observed when more lenient thresholds for cluster level analysis were employed.

General discussion

Our study focused on judgments of semantic relations between linguistic items. We tested the hypothesis that the open-ended nature of metaphoric sentences will affect relatedness judgments in a way different from that of literal sentences that are deemed less conducive to multiple possible interpretations. In particular, we expected probes in the metaphoric but not in the literal condition to prompt an extensive search for relatedness prior to rejecting a semantic relationship. Our findings support this view. They show that relatedness judgments are influenced by the open-endedness of the prime, as indicated by the different neural substrates involved in the metaphoric and literal conditions.

Specifically, our data support our prediction that judgments of relatedness to metaphoric statements would lead to activation in right frontal cortical areas, as demonstrated by the increased BOLD signal in the right ventrolateral prefrontal cortex for the metaphoric category. We view this finding as reflecting a basic qualitative difference between literal and metaphoric context effects stemming from the different degrees of open-endedness between metaphoric and literal statements.

To test our hypothesis, we designed a study that differs in several of its aspects from previous ones investigating the neural substrates of figurative language. Hitherto, most studies have focused on either implicit or explicit extraction of meaning from sentences (Rapp et al., 2004; Stringaris et al., in press), or on discovering metaphoric/literal meaning relation between single words (Lee and Dapretto, in press; Mashal et al., in press). In this experiment, we attempted to test a linguistic operation closer to natural language use, where subjects look for a relationship between a linguistic stimulus and the information they have recently processed. Thus, our study did not explicitly require extraction of meaning from the sentence presented, nor did it necessitate the construction of an ad hoc metaphoric or literal category to explain the relationship between two words. Rather, metaphoricity and literality were treated as given whereas what was assessed here was the degree to which a word currently being processed was perceived as related to a previously processed sentence context.



Fig. 1. Activations in the Right Frontal Cortex: (a) rejection of words preceded by a metaphors, compared to the literal condition (IRM>IRL); (b) rejection of a word following literal sentences (IRL>IRM) compared to the metaphoric condition; (c) endorsement of words preceded by metaphors, compared to the literal condition (RM>RL); (d) endorsement of words following literal sentences compared to the metaphoric condition (RL>RM). Note that the right side (R) of this picture corresponds to the viewer's left hand side. N=12, activations observed at voxel p value <0.05, cluster p value <0.0025.

Importantly, this study differs from others in that it concentrates on the influence of metaphoricity when rejecting a semantic relationship. Focusing on rejection has several methodological advantages. Firstly, rejection cannot be confounded by eureka! or aha! effects, which are known to elicit neural responses on their own accord (Luo et al., 2004b). Second, to maximize comparability, in the present study the unrelated probe was identical for both the metaphoric and literal conditions, thereby excluding the possibility that differences in responses or in the neural substrate they activate might originate in the word itself rather than in the type of relationship it evokes in the context of the sentence that precedes it. This, however, is not true of the endorsement task, where probes can hardly be the same in both conditions. These differences between the two sides of the task is probably reflected in the finding that although it took subjects similarly long to reject words as unrelated following both literal and metaphoric sentence contexts, it took subjects significantly longer to endorse metaphoric relations compared to literal ones. In addition, subjects made significantly more errors when they had to endorse a figurative rather than a literal relationship. However, both response times and the number of errors did not differ across conditions when subjects had to reject a semantic relationship. This finding is crucial as it suggests that the differences observed in brain activation are not the result of varying levels of difficulty between the two conditions but are more likely to reflect different types of cognitive processing.

In humans, the frontal lobes and the prefrontal cortex in particular are crucial in a number of cognitive tasks, most notably those involving executive functions and cognitive control (Lezak et al., 2004; Miller, 2000; Seitz et al., 2000). In language tasks, prefrontal regions are implicated in controlled semantic retrieval and selection (Gold and Buckner, 2002; Thompson-Schill et al., 1997). In our study, we found that rejecting semantic relationships, primed by metaphoric but not by literal sentences, led to activations in the right ventrolateral prefrontal cortex. One influential theory of brain processing in language comprehension contends that the RH performs more coarse computations, in the sense that wider inputs and outputs in the RH lead to more diffuse semantic activations compared to the left hemisphere (Jung-Beeman, 2005). The coarse semantic coding theory would account for the fact that when subjects are presented with unusual semantic items, such as novel metaphors, the RH becomes increasingly involved (Mashal et al., 2005, in press). We note that in previous studies (Kircher et al., 2001), rather than the right frontal areas found in our study, the right temporal cortex was shown to be activated in a task involving processing of linguistic context of literal sentences. This difference may be accounted for by the type of task used. In Kircher et al. (2001) subjects were expected to generate an appropriate word to complete a clause, whereas in our study subjects had to make judgements about the semantic relationships of items that were presented to them. Similarly, in a recent event-related potential (ERP) investigation (Sotillo et al., 2005) augmented by spatial analysis and using a task design similar to the one used in the present study, it was found that right temporal but not right frontal activation was involved in the processing of metaphoric items. It is important to note, however, that their study employed novel metaphoric priming sentences, whereas in our study rather conventional priming items were used.

Even though the metaphoric sentences used in this study involve more conventional than novel metaphors - in fact, when presented as part of a meaningfulness task in previous experiments, they led to predominantly left hemispheric and left thalamic activations compared to literal sentences (Stringaris et al., in press) - our findings may still be viewed as consistent with both the coarse coding and graded salience models. According to the graded salience hypothesis (Giora, 1999, 2003), not only novel, but also familiar metaphors give rise to multiple meanings. Conventional metaphors make available their salient (literal and metaphoric) meanings; novel metaphors make available their salient (literal) and novel (metaphoric) interpretations. Once such meanings are activated, they may affect ongoing processes and result in an extensive and complex search for relatedness, especially in the presence of remotely related probes, which, in our study, would eventually have to be rejected as unrelated. On account of their open-endedness, then, metaphors might induce complex associations with oncoming messages. Such associations will be processed in the RH, as also predicted by the coarse coding theory (Jung-Beeman, 2005).

The task presented here required relatedness judgements. We suggest that searching for semantic relations involves activation of a different range of properties than those involved in simply extracting the meaning of a sentence and probably requires access and hence activation of a number of different meanings with varying degrees of salience and of semantic remoteness. Thus, the results of these studies demonstrate that the very same linguistic items may lead to different brain activations depending on the type of cognitive operation. the right frontal cortex reflect the attempt to establish a semantic relationship between items. Crucially, although activation in the right frontal cortex was shown for both literal and metaphoric sentences when semantic relationships were endorsed (albeit in adjacent but not in identical peaks of cluster activation), it was the rejection side of the task that discriminated between the effects of the literal and metaphoric condition; rejecting a probe following a metaphoric sentence involved the ventrolateral prefrontal cortex when compared to the literal condition. Why should right hemispheric activation occur only in the metaphoric condition when rejection of relatedness is considered? A recent divided visual field priming study (Kacinik and Chiarello, in press) has shown that although the right hemisphere may not be preferentially involved in metaphor comprehension, it serves to maintain a greater number of alternative interpretations compared to the left cerebral hemisphere, as evidenced by the finding that sententially inappropriate literal targets could be primed by inconsistent metaphoric sentences. The authors suggest that metaphor processing requires the integration of very different conceptual domains where it is less evident which semantic aspects will eventually be relevant for interpretation. Further evidence about a differential processing between metaphors and literal sentences comes from Coulson and Van Petten (2002) using an event-related potential (ERP) paradigm. The authors reproduced the larger N400 amplitudes for metaphoric as compared to literal items observed previously (Pynte et al., 1996) and argued that this may be the result of subjects having to establish mappings between elements in distantly related domains in the metaphoric condition. We propose that properties inherent to metaphoric sentences such as open-endedness may account for such differences. Although providing a full fledged account of open-endedness will clearly require additional empirical data and conceptual elaboration, we assume that open-ended items are susceptible to more than one potential interpretation and hence are more likely to allow for a greater number of semantic relationships, some of which will become evident only if sufficiently primed. In Richard Boyd's words, users of metaphors are typically unable to precisely specify the relevant aspects of similarity or analogy (Boyd, 1993). Similarly, Martinich (2001) argues that aspects of metaphoric indeterminateness prompts listeners to "look for relationships between things not previously encountered". In linguistic terms, one could argue that the conceptual boundaries of metaphors are "more elastic and permeable" than those of literal sentences (Black, 1993) and that figurative statements evoke a wider range of entailments than their literal counterparts (Gibbs, 1992). This would mean that, in our experiment, judging relatedness to a metaphoric sentence context elicits a search in a more widely spread semantic network even when the word under scrutiny is eventually assessed as unrelated. By virtue of their openendedness, the metaphoric sentence contexts in this study bias cognitive processing towards a wider search, permitting more semantic relationships to be activated in the RH. In contrast, the literal sentences in our study, which were probably perceived as being more circumscribed than the metaphors, would lead to an initially narrower search within the left hemisphere (LH). Indeed, rejecting words as irrelevant following literal sentences led to activations in several areas of the LH previously implicated in language processing, such as the angular gyrus (Booth et al., 2003) and the inferior parietal lobe (Gold and Buckner, 2002). Although our study is addressing the issue of metaphoric open-endedness,

The results of this study suggest that the activations observed in

the possibility that other types of sentences, including certain types of literal sentences, might also be processed as open-ended statements seems appealing and would lend itself to empirical testing.

A question arising from the results of the present study is why RH activation was observed when, following a literal sentence, a target word was endorsed but not when the target word was rejected. It has been suggested that when an item is perceived as unrelated no further search for affinities is initiated (Rosch, 1999) and is thought to be processed in the left hemisphere (Faust and Gernsbacher, 1996). Thus, following the semantically more circumscribed literal sentences in our paradigm, perceiving an item as unrelated did not activate a further search for contextual affinities. Conversely, when an item was perceived as related the attempt of fitting it into the given literal sentence context led to RH activation. Although this may be a likely explanation of our findings, it is clearly post hoc and requires further empirical testing.

In addition to providing further evidence in favor of metaphoric open-endedness, our data demonstrate that brain imaging is particularly useful in highlighting differences between cognitive processes, even when behavioral data, in this case, response times, are equal across categories. Our data also shed further light on the role of the RH and are in agreement with the coarse semantic coding theory (Jung-Beeman, 2005). The search for establishing distant semantic relationship, in this study between a sentence context and a word, involves activation of areas in the right frontal cortex for both metaphoric and literal sentences. However, it is only the metaphoric context that biases processing towards a search for semantic relatedness even when this is eventually rejected and this is reflected by activation of the right ventrolateral prefrontal cortex. Also, it becomes increasingly clear from this and previous studies that the degree of right hemispheric involvement in language processing is contingent upon a number of factors, most notably the type of cognitive task involved, the type of condition involved, e.g., metaphoric versus literal, as well as the remoteness of semantic relationships.

Taken together, our findings argue in favor of a qualitative difference between metaphoric and literal conditions in terms of their effects on judgments of semantic relatedness. We suggest that this can be accounted for by the open-ended nature of metaphoric items. We propose that open-endedness is not a concept to be traced in one particular anatomical location, but like metaphors, it should be viewed as an important linguistic variable, which can influence cognitive processing within the constraints of a given task and hence could be conceivably reflected in various neuroanatomical networks. Further empirical studies to assess the validity of this construct, perhaps through specific task manipulation to evoke different degrees of open-endedness, could prove particularly informative.

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