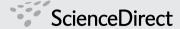
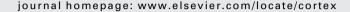


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Research report

Neural differences in the processing of true and false sentences: Insights into the nature of 'truth' in language comprehension

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ABSTRACT

The inquiry on the nature of truth in language comprehension has a long history of opposite perspectives. These perspectives either consider that there are qualitative differences in the processing of true and false statements, or that these processes are fundamentally the same and only differ in quantitative terms. The present study evaluated the processing nature of true and false statements in terms of patterns of brain activity using event-related functional-Magnetic-Resonance-Imaging (fMRI). We show that when true and false concept-feature statements are controlled for relation strength/ambiguity, their processing is associated to qualitatively different processes. Verifying true statements activates the left inferior parietal cortex and the caudate nucleus, a neural correlate compatible with an extended search and matching process for particular stored information. In contrast, verifying false statements activates the fronto-polar cortex and is compatible with a reasoning process of finding and evaluating a contradiction between the sentence information and stored knowledge.

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1. Introduction

The inquiry on the nature of truth in language comprehension has a long history that can be traced to the ancient Greek philosophers, with Protagoras defending that "man is the measure of all things" and Socrates criticizing his relativism. In the last decades philosophers have mainly sided up with Protagoras, emphasizing that truth cannot be objectively defined, but rather is relative to the individual who claims it (Blackburn, 2005).

In empirical terms this debate is related to the process of online language comprehension, where the meaning of a sentence is derived and its truth verified. In this context, a similar opposition can be found between perspectives that either consider that there are qualitative differences in the processing of true and false statements (i.e., true and false statements involve different mechanisms or processes) or consider that these processes are fundamentally the same and only differ in quantitative terms (i.e., true and false statements are similarly processed and only differ in terms of

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level of activation). The latter relativist position finds support in behavioral studies showing that the time required to process true and false statements depends on the strength of the relation between the concept and the property that is being evaluated (e.g., "the dog has four legs"). More specifically, independently of their true/false status, the stronger the relation between property and concept, the quicker the answer in terms of reaction time (RT) (Hutchinson and Lockhead, 1977; Rips et al., 1973).

The possibility of qualitative different processes for verifying true and false sentences remains an open question. In fact, in our daily lives the distinction between true and false statements is usually more subtle and not reducible to ambiguity or relation strength. Moreover, this relation strength in terms of subject–predicate can be controlled across true and false sentences. This control can be achieved by using true and false sentences where subject and predicate are semantically related which results in no RT or small RT differences between the two types of sentences (McCloskey and Glucksberg, 1979). What may happen in this situation? Would it be possible then to find any qualitative distinction or marker of true us false sentences processing?

Some behavioral studies suggest that true and false information are initially represented as true (Gilbert et al., 1990, 1993). Next, other studies suggest that deciding that a sentence is true may just involve finding the sentence information in memory, while deciding that it is false may involve finding a contradiction between the sentence information and stored knowledge (e.g., Collins and Quillian, 1969; Glass et al., 1974). In the first case, the task may be similar to the recall or recognition of a specific memory trace, while in the second case it may require reasoning or problem-solving. However, the discussion about this possibility has been long forgotten amidst the decline of interest in semantic memory as related to sentence verification tasks (Chang, 1986). Moreover, since neither the qualitative or quantitative models completely accounted for all the observed data, each was modified in order to achieve this goal. The result was that in many instances it became very difficult to tell the two views apart from behavioral data (Murphy, 2004).

With the development of imaging techniques it is now feasible to explore the neural correlates of language processing and in this way evaluate alternative cognitive theories on the basis of brain activation patterns (e.g., Cappa, 2006; Umiltá, 2006; Vallar, 2006; but see Coltheart, 2006 for an opposing view). The relativist position finds support in terms of patterns of neural activity from a recent paper by Hagoort et al. (2004). These authors have shown that true and false sentences increase the activation of the same brain regions in the left inferior frontal cortex (BAs 45 and 47) in comparison to a low-level baseline. Moreover, the activation in these regions was higher for false than for true sentences. This quantitative difference may be interpreted in terms of false sentences requiring extra processing, as they provide information that is more ambiguous or uncertain as compared to true sentences. In accord with this interpretation are also results showing increased activation in BA 45 for sentences containing ambiguous words relative to sentences with unambiguous words (Rodd et al., 2005). On the other hand, different patterns of brain activity have been recently reported by Harris et al.

(2008) for true, false and undecidable statements from a wide range of contents (e.g., geographical, mathematical, semantic synonyms, autobiographical). True compared to false statements activated the ventromedial frontal cortex, while the reverse comparison engaged the left inferior frontal gyrus, anterior insula, dorsal anterior cingulate and superior parietal cortex. When the statement was undecidable (such as "you had eggs for breakfast on Dec 8th, 1999"), the contrast with true and false statements showed an increased activity in the anterior cingulate, and a deactivation of the caudate nucleus (Harris et al., 2008). However, the study did not control for sentence ambiguity and the fact that true statements were verified more rapidly than false statements is certainly related to this lack of control. Moreover, the study did not evaluate for common activations or for differences within these common activations and, as such, does not allow us to compare the two alternative theories.

The present study examined the impact of true and false sentences on brain activity with a feature verification task and fMRI. Participants read simple sentences composed of a concept-feature pair (e.g., 'the plane lands') and decided whether the sentence was true or false. True and false statements were equated in terms of concept-feature relation strength and exactly the same concepts and features were used across the two types of sentences. As such, similar to McCloskey and Glucksberg (1979), we expect no significant RT differences, or small RT differences, between the two types of sentences. Furthermore, if processing true and false sentences involves only a single process then we expect that the difference between the two conditions will be apparent in quantitative terms within the commonly activated regions. Alternatively, if processing true and false sentences involves qualitative processing differences instead of a single process, we expect that these will be reflected in the activation of incompletely overlapping brain activity patterns (Cappa, 2006).

2. Method

2.1. Participants

Twenty-one healthy right-handed (Oldfield, 1971) participants, native speakers of Italian (9 males, 12 females; mean age = 26.09 years, SD = 1.89, range = 24-29) took part in the study. All subjects had normal or corrected-to-normal visual acuity. All reported no history of psychiatric or neurological disorders, and no current use of any psychoactive medications. Participants gave informed written consent to the experimental procedure, which was approved by the local Ethics Committee.

2.2. Experimental design and materials

The experiment involved a single within-subjects design, where statement status was true or false. Statements were composed of concept–features pairs embedded in a simple sentence: concept X has/is feature Y (e.g., 'The bottle floats'). Concepts regarded animals and objects, and features were either visual form/surface or motor/action features in equal

proportions (see Table 1 for examples). A list of 336 stimuli was selected from a larger database of 838 concept-feature pairs rated on 4-point rating scale by a total of 83 participants (that otherwise did not participate in the study). Each of the 838 concept-feature pairs was rated by a mean of 18 participants of the total group (n = 83) on how the feature described was more or less relevant for the concept (from always false to always true of the concept). Stimuli were chosen so that they were judged mainly true or false but not in absolute terms (i.e., stimuli with a mean relevance of either 4 or 1) as a first control of relation strength. A first behavioral pilot of the experimental task with this list (i.e., the participant had to decide whether the statement presented was true or false, and press a corresponding button) showed that some of the selected stimuli (15 false and 7 true) had in fact low hit rates (lower than 50%) and these were interchanged or modified, totaling 22 new concept-feature pairs that were not further rated in terms of relevance. Other than that, hit rates and reaction times were equated between true and false conditions [t(312) = 1.35, p = .18 for hits; t(312) = 1.64, p = .10 for RT], whichprovided a second control of relation strength across true and false sentences. The final list of stimuli, that was used during fMRI scanning, included 336 concept-feature pairs, half of which were true statements and half false. In the final list (data only for 312 items), stimuli were differently judged as true (mean relevance = 3.27) or false (mean relevance = 1.39), t(312) = 34.22, p < .01, but equated in terms of relation strength as assessed by hit rates and reaction times. As the concepts and features were exactly the same in the two experimental conditions, the conditions were automatically matched in terms of psycholinguistic variables.

Each concept-feature pair was embedded in a simple sentence (e.g., 'The bottle floats') that appeared on screen for 2800 msec; the participant had to decide whether the statement presented was 'generally' true or false of the concept, and press the corresponding button with their left hand (middle finger for true, index finger for false). Sentences were presented with the definite determiner (the) and it was emphasized that their judgment of true or false should be made considering if the feature generally or typically applied to the concept (e.g., 'the bottle floats'). This formulation was chosen instead of one with the indefinite determiner (a), as pre-test of the materials

Table 1 – Examples of true and false statements (Italian original and English equivalent).

True statements False statements La giraffa è alta/ The giraffe is tall L'ambulanza è veloce/ The ambulance is fast L'asino è grigio/ The donkey is grey La bottiglia galleggia/ The bottle floats L'auto sportiva ha l'antenna/ The sports car has an antenna Il cavallo gareggia/ The horse competes

La spada è alta/ The sword is tall La lumaca è veloce/ The snail is fast Il cammello è grigio/ The camel is grey Il martello galleggia/ The hammer floats La spilla ha l'antenna/ The pin has an antenna Lo scoiattolo gareggia/ The squirrel competes

showed that the latter induced participants to judge almost every sentence as false (e.g., it is always possible to think of a particular bottle that does not float). A baseline condition was added to the experimental conditions. This corresponded to 42 strings of '+' (e.g., +++++++++++++) that appeared on screen for 2800 msec; the participant had to press a button (left finger) for each presented string. The study was composed of seven scanning periods lasting about 6 min 40 sec each, that begun with a 500 msec ready sign ("Ready"). Each scanning period was composed of 24 concept-feature pair sentences that were randomly selected from each of the two experimental conditions, plus the baseline (total of 54 items per scanning period). The order of presentation of both conditions and stimuli within each scanning period, and the order of presentation of the seven scanning periods, were completely randomized for each subject. Successive trials were separated by a variable inter-stimulus interval. In order to optimize statistical efficiency, inter-stimulus intervals between successive trials within a block were presented in different ("jittered") durations across trials (2850, 5850 and 7850 msec, in proportion of 4:2:1) (Dale, 1999). Stimulus pairs were viewed via a back-projection screen located in front of the scanner and a mirror placed on the head coil. Stimulus pairs were presented, and subjects' answers and experimental timing information were recorded, using the software Presentation 9.13 (http://nbs.neuro-bs.com).

2.3. Data acquisition and analysis

Anatomical T1-weighted and functional T2*-weighted MR images were acquired with a 3 T Philips Achieva scanner (Philips Medical Systems, Best, NL), using an 8-channel Sense head coil (sense reduction factor = 2). Functional images were acquired using a T2*-weighted gradient-echo, echo-planar (EPI) pulse sequence (30 interleaved slices parallel to the Anterior Commissure-Posterior Commissure [AC-PC] line, covering the whole brain, TR = 2000 msec, TE = 30 msec, flip angle = 85 degrees, $FOV = 240 \text{ mm} \times 240 \text{ mm}$, no gap, slice thickness = 4 mm, in-plane resolution $2 \text{ mm} \times 2 \text{ mm}$). Each scanning sequence comprised 200 sequential volumes. Immediately after the functional scanning a high-resolution T1-weighted anatomical scan (3D, SPGR sequence, 124 slices, TR = 600 msec, TE = 20 msec, slice thickness = 1 mm, in-plane resolution 1 mm × 1 mm) was acquired for each subject.

Image pre-processing and statistical analysis were performed using SPM5 (Wellcome Department of Cognitive Neurology, http://www.fil.ion.ucl.ac.uk/spm), implemented in Matlab v7.1 (Mathworks, Inc., Sherborn, MA) (Worsley and Friston, 1995). The first 5 volumes of each subject were discarded to allow for T1 equilibration effects. EPI images were realigned temporally to acquisition of the middle-slice, spatially realigned (Friston et al., 1996) and unwarped (Andersson et al., 2001). The anatomical T1-weighted image, coregistered to the mean of the realigned EPI images, was segmented into grey and white matter, and the grey-matter normalized image was spatially (voxel size: $2 \text{ mm} \times 2 \text{ mm} \times 2 \text{ mm}$) (Ashburner and Friston, 1999) to a grey-matter template (http://www.loni.ucla.edu/ICBM/ ICBM_TissueProb.html). The resulting deformation parameters were then applied to all the realigned and unwarped

functional images, which were finally spatially smoothed (Full-Width–Half-Maximum [FWHM] Gaussian kernel: $6~\text{mm} \times 6~\text{mm} \times 6~\text{mm}$) and globally scaled to 100. The resulting time-series across each voxel were then high-pass filtered to 1/128 Hz, and serial autocorrelations were modeled as an auto-regressive [AR(1)] process.

Statistical maps were generated using a random-effect model (Friston et al., 1999), implemented in a two-level procedure. At the first level, single-subject event-related fMRI responses, synchronized with the acquisition of the middleslice, were modeled as delta "stick" functions by a designmatrix comprising the middle point between the onset of the stimulus and the motor true/false response for each trial of all experimental conditions. Only those trials in which subjects gave a correct response were modeled as belonging to a given task, whilst all the other trials, independently of the experimental condition, were modeled in a separate regressor. Regressors modeling events were convolved with a canonical Haemodynamic Response Function (HRF), along with its temporal and dispersion derivatives, and parameter estimates for all regressors were obtained by maximum-likelihood estimation. Contrasts of parameter estimates were then calculated to produce "contrast images" for the contrast of interest ("True minus baseline"; "False minus baseline").

At the second (group) level, these contrast images from all subjects were separately entered into one-sample t-tests to highlight the regions activated in each of the two tasks separately. Then we investigated the regions that were commonly activated by both true and false sentence processing by using a conjunction analysis (conjunction-null; Nichols et al., 2005) on the "True minus baseline" and "False minus baseline" statistical maps.

The same first-level contrast images were finally entered into paired-sample t-tests to investigate significant differential activations between conditions ("True minus baseline" vs "False minus baseline"; "False minus baseline" vs "True minus baseline"). The resulting statistical maps were masked at p < .05 uncorrected by that of the conjunction analysis either (a) inclusively, to highlight the regions showing significant differences between the two tasks within those commonly activated (i.e., reflecting quantitative differences in processing true and false statements) or (b) exclusively, to highlight the regions showing significant differences between the two tasks outside those commonly activated (i.e., reflecting qualitative differences in processing true and false statements).

All the statistical maps were thresholded at p < .05, Family-Wise-Error (FWE) corrected for multiple comparisons, and only cluster larger than 5 contiguous voxels were considered.

For anatomical localization, the functional data were referenced to probabilistic cytoarchitectonic maps of the human brain, using the SPM-Anatomy toolbox (Eickhoff et al., 2005). The thereby probabilistically assigned foci are denoted by an asterisk both in tables and in Section 3 for the cerebral regions of which cytoarchitectonic probabilistic maps are provided.

3. Results and discussion

The results for the effects of category domain and feature type have been reported in Marques et al. (2008).

Total mean hit rate was 90.5%, and only six items (1.7% of the items) presented a hit rate lower than 50%. When we analyzed hit rate by true vs false items, no significant differences were found $[F(1,334)=.30,\,p<.58]$. Reaction times were also analyzed by true vs false items using a similar one-way ANOVA, after trimming the data for incorrect answers and for outliers, defined as two standard deviations above each subject mean response time (corresponding to the elimination of 12.4% of the data which is within the normal recommended limits; Ratcliff, 1993). Again in this case no significant differences were found between true and false sentences $[F(1,334)=1.24,\,p<.27]$. These results thus confirm that true and false sentences used in the study are comparable in terms of concept–feature relation strength or overall sentence ambiguity.

In terms of imaging results we first examined the cerebral regions activated in the two experimental conditions (against the baseline: True minus baseline, False minus baseline; Fig. 1, top and middle panel, and Table 2) and those resulting from a conjunction analysis of the baseline contrasts (Price and Friston, 1997) (Fig. 1, bottom panel and Table 2). Overall, the conjunction analysis highlighted a network of commonly activated regions which included the inferior and middle occipital gyri (BA 18/19) along with the fusiform gyrus (BA 37) bilaterally, and the posterior middle temporal gyrus (BA 37/21) in the left hemisphere. An extensive cluster, extending from the middle occipital gyrus, through the superior parietal lobule, to the inferior parietal lobule was also activated in the left hemisphere. In the frontal lobe, the pre-supplementary motor area (pre-SMA) and SMA-proper (BA 6*) were activated within the medial wall. In addition to these regions, all the experimental conditions activated a wide frontal cluster in the left hemisphere, extending from the precentral gyrus (BA 6) and the middle frontal gyrus (BA 6) to the fronto-insular cortex. Within the inferior frontal gyrus, common activations were observed in the pars opercularis (BA 44*), pars triangularis (BA 45*) and pars orbitalis (BA 47) (Fig. 1, bottom panel and Table 2). In the right hemisphere, frontal activations were observed in the fronto-insular cortex, including the insula lobe and the pars orbitalis (BA 47) of the inferior frontal gyrus, as well as in the dorsal portion of the pars triangularis (BA 45*) and in the middle frontal gyrus (BA 46). Finally, common subcortical activations were observed in the left hippocampus*, and in the putamen bilaterally.

This common activated network is consistent with several neuroimaging studies of language that demonstrated differential activation patterns and a left-lateralized large-scale network for semantic processing (see for example McDermott et al., 2003). Moreover, this network also included the regions in the left inferior frontal cortex (BAs 45 and 47) previously signaled by Hagoort et al. (2004) and by Rodd et al. (2005) as related to semantic processing.

Turning to the differences between tasks, when we evaluated the results of the direct comparisons between the true and false conditions within the commonly activated regions (i.e., by inclusive masking with the conjunction analysis) no significant differences were found. Along with the absence of significant differences with regard to both RT and hits-percentage at the behavioral level, this result further shows that in the present situation, where concept–feature relation strength or ambiguity

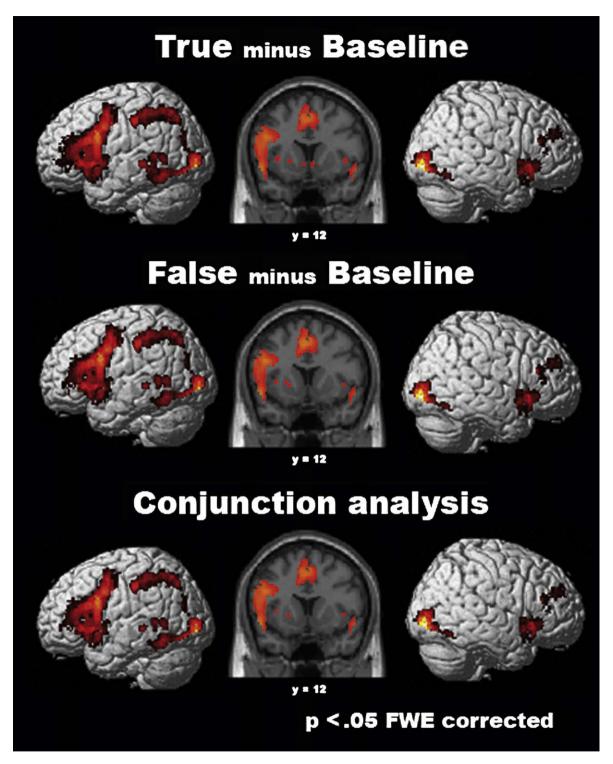


Fig. 1 – Imaging results: true and false statements and conjunction analysis. From top to bottom, the cerebral regions that were activated in association with processing true statements (minus the baseline; A), processing false statements (minus the baseline; B) and in both experimental conditions (conjunction analysis; C) are shown (p < .05 Family-Wise-Error corrected for multiple comparisons, minimum cluster-size = 5 voxels). Activations were superimposed onto 3D-renderings of the MNI template and one representative coronal slice (y = 12) showing subcortical structures of interest.

was controlled for, the neural processing of true and false statements is not reflected by quantitative processing differences. Considering that nevertheless the regions previously found to be related to the integration word meaning and world knowledge

(BAs 45 and 47; Hagoort et al., 2004) were activated, it can be concluded that in this situation of controlled concept–feature relation strength their involvement is not sufficient to decide whether a sentence is true or false.

Gyrus (46)

Putamen

Hippocampus

Caudate nucleus

Caudate nucleus

Fronto-polar cortex

R

L

L

R

R

| Н | Conjunction analysis Anatomical region (BA) | АТр | K | MNI | | | Z-score | True | False |
|-----|--|-----|------|-----------------|----------|----------|--------------|--------------|------------|
| | | | | Х | у | z | | Z-score | Z-score |
| L | Inferior occipital gyrus (19) | | 1629 | -38 | -80 | -8 | >8 | >8 | >8 |
| | Middle occipital gyrus (18) | 20 | | -22 | -92 | -2 | >8 | >8 | >8 |
| | Fusiform gyrus (37) | | | -34 | -46 | -24 | >8 | >8 | >8 |
| R | Inferior occipital gyrus (19/37) | | 788 | 40 | -64 | -12 | 6.89 | 6.89 | 7.04 |
| | Fusiform gyrus (37) | | | 36 | -62 | -18 | 7.14 | 7.14 | 7.26 |
| L | Middle temporal gyrus (37/21) | | 171 | -56 | -56 | 6 | 7.12 | 7.12 | 7.30 |
| | Middle temporal gyrus (21) | | | -52 | -34 | -2 | 5.87 | 6.07 | 5.87 |
| L | Middle occipital gyrus (19) | | 1288 | -28 | -70 | 26 | >8 | >8 | >8 |
| | Superior parietal lobule (7) | | | -24 | -66 | 46 | >8 | >8 | >8 |
| | Inferior parietal lobule (40) | | | -28 | -58 | 46 | >8 | >8 | >8 |
| | Inferior parietal lobule (40/2) | | | -44 | -28 | 42 | 7.30 | 7.30 | 7.78 |
| L/R | SMA (6*/32) | 50* | 1463 | -6 | 8 | 50 | >8 | >8 | >8 |
| | SMA (6*) | 90* | | 8 | -4 | 66 | 5.23 | 5.23 | 5.33 |
| L | IFG-pars opercularis (44*) | 50* | 2964 | -48 | 8 | 28 | >8 | >8 | >8 |
| | IFG-pars opercularis (44*) | 50* | | -54 | 12 | 16 | >8 | >8 | >8 |
| | IFG-pars triangularis (45*) | 70* | | -54 50 | 22 | 24 | >8 | >8 | >8 |
| | IFG-pars triangularis (45*) IFG-pars orbitalis (47) | 60* | | -50 -44 | 38 18 | 8 -12 | 7.76 6.72 | 7.79 7.04 | >8 6.72 |
| | Insula lobe | | | - 31 | 18 | 6 | 7.12 | 7.54 | 7.12 |
| | Precentral gyrus (6) | 10 | | _50 | 4 | 40 | >8 | >8 | >8 |
| | Middle frontal gyrus (6) | 30 | | -28 | -4 | 48 | 7.76 | 7.78 | 7.84 |
| | Putamen | | | -22 | 18 | -2 | 5.89 | 5.90 | 5.97 |
| R | Middle frontal gyrus | | 100 | 42 | 42 | 26 | 7.63 | 7.63 | >8 |
| R | IFG-pars orbitalis | | 390 | 40 | 24 | -16 | 5.78 | 5.78 | 5.81 |
| | Insula lobe | | | 32 | 28 | -4 | >8 | >8 | >8 |
| R | IFG-pars triangularis (45*) | 50* | 68 | 52 | 36 | 14 | 6.29 | 6.29 | 6.86 |
| | IFG-pars triangularis (45*) | 40* | | 52 | 38 | 8 | 6.54 | 6.54 | 7.11 |
| | IFG-pars triangularis/MFG (45) | 20 | | 50 | 34 | 22 | 6.68 | 6.91 | 6.68 |
| | Middle Frontal | | | 36 | 44 | 32 | 7.39 | 7.39 | 7.60 |

Stereotactic coordinates and Z-scores of the foci of maximum activation for processing of both true (minus the baseline) and false (minus the baseline) sentences (conjunction analysis) are shown (p < .05, Family-Wise-Error corrected for multiple comparisons). Coordinates are expressed in MNI space adopted by SPM5 in terms of distance in mm from the anterior commissure. H, hemisphere; L, left; R, right; BA, estimated Brodmann Area; ATp, probability associated with the anatomical region (where cytoarchitectonic probabilistic maps are available) according to the Anatomy Toolbox (Eickhoff et al., 2005; asterisks denote assignment), K, cluster-extension in number of voxels ($2 \times 2 \times 2 \text{ mm}^3$); SMA, Supplementary Motor Area; IFG, Inferior Frontal Gyrus. The Z-scores of the same local maxima in each of the two tasks are also shown, in the rightmost columns of the table.

22

-22

-8

6

36

20

-34

16

12

50

-2

-4

-4

20

5.87

>8

5.87

5.65

6.31

6.01

>8

4.79

24

145

12

421

5

40*

In contrast, when we evaluated the differences between the true and false conditions outside the commonly activated regions (i.e., by exclusive masking with the conjunction analysis) we found significant differences in the pattern of brain activity associated to the processing of these two classes of statements (see Table 3 and Fig. 2).

False statements differentially activated the right frontopolar cortex (BA 46 and 10) in areas that have been previously related to reasoning tasks, namely to relational integration (Christoff et al., 2001) and to relational complexity (Kroger et al., 2002). These regions are activated by demanding reasoning tasks, and the right fronto-polar cortex is most likely associated with the processing of self-generated information (Christoff et al., 2001). This is consistent with the hypothesis that processing false statements may be a case of problem-solving that involves finding a contradiction between the sentence information and information stored in memory (Collins and Quillian, 1969; Glass et al., 1974). This increased activation for false statements may reflect the fact that their similar ambiguity in comparison to true statements constitutes a more demanding task, requiring the additional involvement of this region to the commonly activated network for language comprehension.

The activations related to true statements involved the left inferior parietal cortex (BA 40) and the caudate nucleus bilaterally. The former activation may be hypothesized to reflect continued thematic semantic analysis and attempts to relate verb affordances and semantic properties of the concept (Kuperberg et al., 2008) in the verification of sentence true status. Another possibility is that this activation is related to an increased engagement of the phonological loop, that both lesion and activation studies have associated to this area (Paulesu et al., 1993; Vallar et al., 1997). This increased activation for true statements may reflect the fact that their similar ambiguity in comparison to false statements requires a more extended memory search and, as such, an increased participation of the phonological loop for short-term memory maintenance. The two interpretations are not mutually

exclusive and are both consistent with the hypothesized search and matching processes associated with processing true statements (Collins and Quillian, 1969; Glass et al., 1974). The caudate activation may also reflect this search and matching processes, as both imaging and patient studies suggest that this region is related to verbal processing fluency (e.g., Butters et al., 1986; Forkstam et al., 2006; Teichmann et al., 2008). In fact, verbal fluency not only involves language production but also crucially depends on effective search processes for information that meets a given criterion (Troyer et al., 1997), similar to the case of processing true statements (Collins and Quillian, 1969; Glass et al., 1974). Finally, this interpretation is also coherent with findings that word retrieval depends on controlled research strategies in the mental lexicon involving prefrontal and striatal structures (e.g., Rosen et al., 2000). Again, the fact that true statements may be more difficult to assess in comparison to previous studies would explain the increased involvement of verbal fluency and controlled research processes for word retrieval. Another possibility is related to the involvement of the caudate nucleus in processing reward-related information, dependent upon an action-reward contingency (Delgado et al., 2000; Tricomi et al., 2003). Recognizing a sentence as true is in itself a positive reward for the subject. This is also suggested by Harris et al. (2008) to explain the involvement of "hedonic" structures, such as the medial prefrontal cortex and the anterior insula in the rejection of false sentences. As in the present study no feedback was given, this result if confirmed extends the role of the caudate in processing reward-related information to a situation where reward is internally generated by the subject.

A possible defense of a quantitative position would be that although true and false statements were equated for concept-feature relation strength, nevertheless their processing could be unique and simply framed in terms of conforming or not with learned rules based on semantic knowledge. In this context, true statements would conform with rules while false statements would violate these rules and hence lead to

| Table 3 – Direct comparisons of true vs false sentences. | | | | | | | | | | | |
|--|--|-----------------------|-----|-----|----|------|--|--|--|--|--|
| Н | Anatomical region (BA) | K | | MNI | | | | | | | |
| | | | x | у | Z | | | | | | |
| | s baseline > False minus baseline (inclusively m ficant cluster | asked by conjunction |) | | | | | | | | |
| | s baseline > True minus baseline (inclusively m ficant cluster | asked by conjunction |) | | | | | | | | |
| True minus | s baseline > False minus baseline (exclusively n | nasked by conjunction | 1) | | | | | | | | |
| L | Inferior parietal lobule (40) | 43 | -52 | -52 | 42 | 5.36 | | | | | |
| | Inferior parietal lobule (40) | | -48 | -48 | 44 | 5.19 | | | | | |
| L | Caudate nucleus | 34 | -10 | 14 | 0 | 5.47 | | | | | |
| R | Caudate nucleus | 40 | 10 | 16 | -2 | 5.73 | | | | | |
| False minu | s baseline > True minus baseline (exclusively n | nasked by conjunction | 1) | | | | | | | | |
| R | Fronto-polar cortex (46/10) | 10 | 28 | 52 | 14 | 5.00 | | | | | |

Stereotactic coordinates and Z-scores of the foci of maximum activation in the direct comparisons between true (minus the baseline) and false (minus the baseline) experimental conditions (p < .05, Family-Wise-Error corrected for multiple comparisons). Coordinates are expressed in MNI space adopted by SPM5 in terms of distance in mm from the anterior commissure. H, hemisphere; L, left; R, right; BA, estimated Brodmann Area; K, cluster-extension in number of voxels ($2 \times 2 \times 2$ mm³).

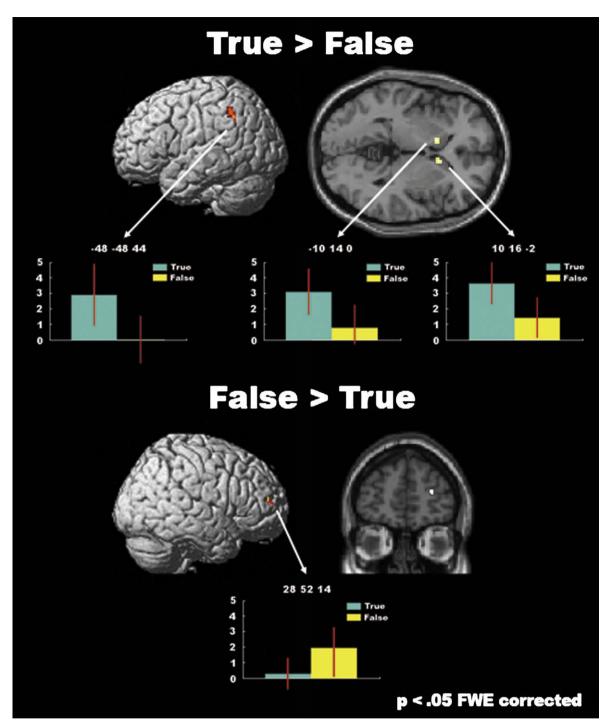


Fig. 2 – Imaging results: direct comparisons true vs false statements. The cerebral regions that were more strongly activated by processing true statements (minus the baseline) than false statements (minus the baseline) (top), and by processing false statements (minus the baseline) than true statements (minus the baseline) (bottom), are shown (p < .05 Family-Wise-Error corrected for multiple comparisons, minimum cluster-size = 5 voxels). Activations were superimposed onto 3D-renderings and representative slices of the MNI template. White arrows link each activated cluster with plots of corresponding condition-specific average parameter estimates (light-blue, true task; yellow, false task; red bars, 90% confidence intervals).

increased activation of rule-based processing. Two main reasons go against this possible explanation. First, the fact that true and false statements were equated for concept-feature relation strength or ambiguity seems to make them more difficult to tell apart in terms of rules and probably

requires more 'instance-based' than 'rule-based' processing. Second, the present results show an increased activation of the caudate nucleus for true statements that imply rule conformity in comparison to false statements that imply rule violation. Crucially, this result is the exact opposite of those

from studies on cerebral activity and rules that tend to show increased activation or involvement of the caudate nucleus for rule violation (e.g., Kuperberg et al., 2008; Teichmann et al., 2008).

More studies are needed to further assess the proposed interpretations of the true- and false-related activations observed in the context of language comprehension and especially to articulate them with a corresponding processing model. Nonetheless, the qualitatively differential pattern of activations obtained in the present study clearly supports the view that the processing of true and false statements involves different processes, at least when their ambiguity level is controlled for. Moreover, considering that the regions previously related to the integration of word meaning and world knowledge (Hagoort et al., 2004) were commonly active in both experimental conditions it can be hypothesized that the differential activations found in the present study correspond to additional processes that are needed to decide whether a sentence is true or false when they are similarly ambiguous and more difficult to distinguish.

Following this perspective it is possible to articulate and reconcile the two ancient and conflicting positions about language comprehension. Paradoxically, it seems that when the differences between truth and falseness are clear-cut we behave like relativists, and use similar processes to arrive at a decision (Hagoort et al., 2004; McCloskey and Glucksberg, 1979). On the contrary, when differences are more subtle like in the present study where concept—eature relation strength was controlled for across sentences, we adhere to a categorical distinction and use qualitatively different processes to decide what is true from what is false (Collins and Quillian, 1969; Glass et al., 1974).

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