



Concrete spatial language: See what I mean?

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Abstract

Conveying complex mental scenarios is at the heart of human language. Advances in cognitive linguistics suggest this is mediated by an ability to activate cognitive systems involved in non-linguistic processing of spatial information. In this fMRI-study, we compare sentences with a concrete spatial meaning to sentences with an abstract meaning. Using this contrast, we demonstrate that sentence meaning involving motion in a concrete topographical context, whether linked to animate or inanimate subjects nouns, yield more activation in a bilateral posterior network, including fusiform/parahippocampal, and retrosplenial regions, and the temporal–occipital–parietal junction. These areas have previously been shown to be involved in mental navigation and spatial memory tasks. Sentences with an abstract setting activate an extended largely left-lateralised network in the anterior temporal, and inferior and superior prefrontal cortices, previously found activated by comprehension of complex semantics such as narratives. These findings support a model of language, where the understanding of spatial semantic content emerges from the recruitment of brain regions involved in non-linguistic spatial processing.

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1. Introduction

It is a challenge to cognitive science to understand how humans are able to exchange and share rich, complex patterns of both physical and social meaning by way of the relatively crude components forming natural language. By simply saying or writing a word (e.g., “house”) we can convey to another person a notion of the entire 3-dimensional structure and functionality of this object. Likewise, if one utters a whole sentence, like: “the man goes through the house,” the hearer will automatically fill in the information needed for comprehension (e.g., that this means going through doorways, not walls).

It is a commonly held hypothesis within cognitive linguistics that basic level words like “house” can convey vastly differentiated meanings only because we hold common knowledge of the world, learned from our interaction with it (Rosch, 1978). Most concepts of objects and events refer to many possible meanings, and a word becomes fully meaningful, only in the context of a whole sentence or a specific reference (e.g., “that house”). This implies that the relevant semantic aspects of a noun like “a man” are very different in relation to a physical object like “a house” compared to an abstract event like “a sorrow.” In “A man goes through a house” the man might first of all be regarded as a physical being abiding to the laws of biophysical motion, while in the sentence like “A man goes through a sorrow” the man is primarily understood as a social agent who behaves

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according to complex norms or narrative “scripts” (Schank & Abelson, 1977).

Human language faculties appear to have emerged very recently, perhaps within the last 300,000 years (Allman, 1999). This short evolutionary time span questions whether neural substrates for linguistic processing are modular and specific to language only (Pinker, 1994), or whether language taps into cognitive systems with a longer phylo- and ontogenetic history (O’Keefe & Nadel, 1978; Talmy, 2000). Research within cognitive linguistics suggests that processing of spatial semantics could be a candidate for the latter type of processing (Talmy, 2000). In Danish and in English, the prepositional markers of spatial relations, such as “over,” “under,” “into,” “through,” etc. are important for structuring semantic content. These markers evoke a schematic relationship between the elements of the sentence known as a “mental space” (Fauconnier, 1994). However, the neural systems used to represent knowledge about topographical properties of the world probably evolved long before language, along with our perceptual and motor capabilities. This opens the question: What is the relation in neural terms between the processing of linguistically based and perceptually based representations of spatial relations?

Most brain imaging experiments on language processes have targeted phonology or speech production rather than processes of meaning formation (for a review, see Price (2000)). This may be due to the complexity of semantics noted above, but studies of linguistic categorical specificity, is one notable exception to this trend. These studies have been based either on a modular theory of conceptualisation (Caramazza, 1998) or on a feature based theory, where linguistic categories are primarily accessed via a specific perceptual modality or specific motor programs—e.g., “tools” (Martin & Chao, 2001; Warrington & McCarthy, 1987; Warrington & Shallice, 1984). From each their perspective, both approaches have attempted to identify the neuronal specificity of broadly defined semantic categories, e.g., “animate” versus “inanimate” beings. However, the results have been very inconsistent (Devlin et al., 2002). A reason for this might be that neither approach addresses the importance of *context* for semantics. In general, meaning is most specific when the context is clearly specified. Therefore, the lexical units of language, i.e., the words, will have more specific meaning, the more linguistic context we add. This interplay between words and context is obviously a crucial mechanism in the workings of language. Although a few studies have investigated neural processing of complex language (Caplan & Dapretto, 2001; Vandenberghe, Nobre, & Price, 2002), to our knowledge no one has systematically targeted the processing of semantic variation imposed by sentence context. We therefore, believe that it is very important to study the relation between neural processes and language comprehension using as the main variable linguistic cues at a whole sentence level.

In this fMRI study, we designed a 2×2 factorial experiment to investigate the neural systems underlying linguistic representations of space, as it unfolds in simple Danish intransitive sentences each containing a grammatical subject, a motion verb and a spatial preposition with a complement noun.

The sentences presented during scanning could have either a concrete (Co) or an abstract (Ab) contextual setting, created by the prepositional complement, while the grammatical subject noun could represent either an animate (An) or an inanimate (In) being. This procedure generated four structurally identical, yet semantically very different, types of sentences, e.g.:

1. An–Co “Manden går gennem huset” (“The man goes through the house”)
2. An–Ab “Manden går gennem sorgen” (“The man goes through the sorrow”)
3. In–Co “Sporet går gennem huset” (“The trail goes through the house”)
4. In–Ab * “Sporet går gennem sorgen” (*“The trail goes through the sorrow”)

A noun in the complement position functions as “ground” in a linguistic figure/ground-configuration (Talmy, 2000). This is also sometimes referred to as the sentence’s “landmark” (Langacker, 1987)—the stable setting against which motion is seen. In An–Co sentences, the landmark is a concrete spatial object, but an abstract noun at this place (e.g., An–Ab sentences) provides the motion verb with a metaphorical meaning where the semantics are less defined in terms of spatial context. Instead it establishes a complex frame of reference that usually implies a social narrative.

The degree of animacy in the subject noun is important for the meaning conveyed by these sentences. An animate entity may be defined as one capable of self-propelled motion. When placed next to a motion verb as in An–Co sentences, the default interpretation is that the animate subject is the one initiating and performing the movement. However, this interpretation is not possible if the grammatical subject is inanimate (In–Co sentences). A large entity like “a trail” cannot be thought of as being forced to move by some other instance. If there is to be any motion in the meaning of In–Co sentences, the movement has to come from somewhere else. Within cognitive linguistics, this phenomenon has been termed “fictive motion” (Talmy, 2000), and it seems that in a fictive motion scenario, the movement originates in the “perceiver” of the event who mentally “scans” or “goes through” that mental space, which is unfolded via the elongated topographical properties of the grammatical subject seen in relation to the contextual landmark of the complement noun.

This dynamic relationship between the first person perspective of perception and the mental space estab-

lished by the linguistic content is stabilised by an interaction with a concrete, imaginable spatial world. Fictive motion sentences therefore, usually become incomprehensible (by linguistic convention marked with an asterisk), when they are combined with an abstract complement noun as in the In–Ab sentences, since this results in a metaphor that can only rarely be attributed with coherent meaning.

We designed a study to investigate brain activations elicited by these four types of sentences when they were either read or heard. Subjects were instructed to indicate with a button press whether they were able to understand the sentence they had just been presented with. Our prior hypotheses were: (a) that sentences with a concrete landmark (An–Co and In–Co) relative to sentences with an abstract landmark (An–Ab and In–Ab) would yield activation in brain regions related to visuo-spatial processing; (b) that fictive motion sentences (In–Co) relative to ordinary motion sentences (An–Co) would elicit more activity in areas related to egocentric space construction; (c) that An–Co sentences might elicit neural activity, which to a higher degree reflect allocentric spatial processing compared to fictive motion; and (d) that An–Ab sentences because of their meaninglessness would result in frontal activation to reflect the inability to integrate the different lexical parts into a congruent meaning.

2. Materials and methods

2.1. Construction of stimulus

We constructed a corpus of Danish intransitive sentences in groups of four by manipulating the subject noun and the prepositional complement noun. As in English, intransitive sentences in Danish have the general outline: NOUN–VERB–PREPOSITION–NOUN. (e.g., “Manden går gennem huset”—[“The man goes/walks through the house”]). Subject nouns were either of an ANIMATE or an INANIMATE sort, and the complement nouns were either CONCRETE or ABSTRACT.

All nouns were held in the singular determinate form, and verbs were all held in present tense. See Section 1 and Appendix A, for examples of the four sentence types. As discussed in Section 1, sentences with inanimate subject and abstract landmark are usually meaningless, at least when presented on their own. This is an emergent effect of the 2×2 factorial design and the fact that in sentence semantics the meaning of each individual word is context dependent.

2.2. Stimulus validation and selection

Before the scanning, a control study was performed to verify the semantic properties of the sentences in each group.

Fourteen students of linguistics University of Aarhus (13 female, 1 male; 20–33 years old) read 4×73 sentences and were asked to rate each on a scale from 5 to 1, where 5 meant “proper Danish,” 4 “acceptable Danish,” 3 “unconventional Danish,” 2 “unacceptable” and 1 “nonsense.”

As discussed previously, In–Ab sentences were generally considered to be meaningless. To ensure that the other three members of the sentence group were easily understandable in Danish, median ratings were calculated for these three sentence types. Only sentence groups with a lowest median higher than or equal to three were let into the final corpus of stimulus sentences.

The students in the control study also evaluated the pool of subject nouns by indicating for each word “animate,” “inanimate” or “do not know.” Animate was defined as “capable of self-propelled motion.” For each sentence, a relative weight between 0 and 1 was calculated as an index of how much the perceived animacy of the subject noun in the sentence differed from the ideal animacy of the group. Briefly, if the subject noun in a particular sentence was evaluated as belonging to the “right” animate/inanimate category, it would be assigned with the number 1, if it was evaluated as belonging to the “wrong” category, it would be assigned with the number 0 while “do not know” nouns were assigned with the number 0.5. An average weight for each sentence was obtained, and only sentence groups with a summed weight higher than 3.5 were allowed to enter the final study. The same procedure was followed with the judgements of concreteness based on an evaluation of the complement nouns as “concrete,” “abstract,” or “do not know.” Concreteness was defined as “something having a physical appearance, for which it is possible to hold an internal image.”

The final corpus of sentences was selected as the 40 highest rated sentence groups from the remaining sentences. The subject nouns in these 160 sentences had a mean rating of animacy of 1 for the animate nouns, and 0.025 for the inanimate nouns, and a rating of concreteness of 0.9723 for the concrete complement nouns, and 0.058 for the abstract. Median ratings of proper language were: animate–concrete, 5; animate–abstract, 4; inanimate–concrete, 5; and inanimate–abstract, 1. This optimised the trade-off noted above between equal ratings on one hand, and the structural identity of the sentences on the other. A one-way ANOVA showed no significant difference ($p < .05$) in average word length between the four noun types in these 40 groups. Animate nouns had an average length of 8.98 letters (SD : 2.81), inanimate nouns 8.53 letters (SD : 2.69), concrete nouns 8.95 letters (SD : 2.46), and abstract nouns 9.15 letters (SD : 2.90).

2.3. Visual and auditory paradigm

Subjects were presented with the same sentences in a reading and a listening paradigm. This was done to elim-

inate modality specific effects in the analysis and allow to focus on modality independent semantic activations only. The order of sessions was randomised across subjects. In both sessions sentences from each of the four groups were presented in blocks of five, amounting to a total of 16s per block (SOA 3.2 s), and a stimulus onset asynchrony of 64s. Within each block, sentences were presented in a pseudo-randomised order to ensure that sentences with the same elements were kept as far apart as possible. Every scan consisted of eight phases of the four blocks amounting to a total scanning time of 8min. 32s per paradigm (+16s of introductory screen).

Stimuli were delivered through Avotech goggles and headphones within the G.E. BrainWave stimulus system. In the reading paradigm, whole sentences were presented in white printing on a black background. For the auditory paradigm the 160 sentences were digitally recorded in an emotionally neutral male voice. There was no significant difference in duration time between the four sentence types when analysed by a one-way ANOVA ($p > .05$) (see Table 1). During the auditory paradigm, subjects were asked to keep their eyes open and to focus on a fixation cross in the middle of their visual field.

Since the experiment only aimed at investigating differences within semantic processing, we did not include a low level baseline condition.

Subjects were asked to report with a button press after each sentence to indicate whether the sentence had been understood (button at right index finger) or not (button at right middle finger) and they were instructed that there were no “correct” answers.

2.4. Subjects

Eighteen volunteers (10 males, 8 females, age range 21–41 years) were scanned. All subjects were right-handed and had no known history of neurological impairment. Ethical approval was obtained from the lo-

cal Committee on Ethics in Biomedical Research (Videnskabetisk Komité for Aarhus Amt) and the volunteers signed a written consent form. One subject was omitted from the data analysis due to excessive movement during scanning.

2.5. Scanning procedure

Subjects were scanned with a 1.5T MR scanner (GE Signa, General Electrics Medical Systems, Milwaukee, WI) at Aarhus Kommunehospital, Denmark. Scans were performed using an echo planar imaging sequence with a 4000ms time of repetition (TR), 40ms time of echo (TE), and 90° flipangle. One hundred and thirty-two volumes were obtained in each session consisting of 48 axial slices with a slice thickness of 3mm and 64 × 64 pixels resolution matrix.

3. Data analysis

3.1. Behavioural data

Responses given up to 800ms after the presentation of a stimulus were considered belonging to the previous stimulus, this allowed for a response window of 4000ms. In the few cases where a subject did not give any response, reaction time was set to 4000ms.

3.2. fMRI data

The data were converted into analyse format using MRIcro (by Chris Rorden, University of Nottingham, UK, <http://www.psychology.nottingham.ac.uk/staff/cr1>), spatially realigned, unwarped, and normalised to an MNI template using Statistical Parametric Mapping (SPM2—Wellcome Department of Imaging Neuroscience, London, UK; <http://www.fil.ion.ucl.ac.uk>) executed in MATLAB (Mathworks, Sherborn, MA, USA). After normalisation the images were smoothed

Table 1

Sentence type	1-An-Co	2-An-Ab	3-In-Co	4-In-Ab
<i>Auditory paradigm</i>				
Sound duration (mean ± SD (ms))	2441 ± 236	2406 ± 223	2380 ± 219	2369 ± 247
Response time (mean ± SD (ms))	2952 ± 293	2967 ± 372	2865 ± 371	2887 ± 348
Response – duration (ms)	511	561	485	518
<i>Visual Paradigm</i>				
Response time (mean ± SD (ms)).	1986 ± 593	2059 ± 610	1985 ± 588	1994 ± 542
Response: “Understood” (%)	89	79	87	13
Response: “Not Understood” (%)	9	19	11	86
No response (%)	2	2	1	1

Mean response time for both the visual and the auditive paradigms. Response time was significantly longer for sentences with an abstract landmark (An-Ab and InAb). Responses show predominance for “understood” answers in An-Co, An-Ab, and In-Co sentences, and an opposite pattern in In-Ab sentences, where inanimate “motion” is coupled with an abstract scenario, yielding semantic incongruity.

with a 12mm FWHM Gaussian filter. A design matrix including both the visual and the audio sessions was made and estimated for each subject. Individual T-contrasts were created from the estimated β -weights and sent to a second level random effects analysis. Significance levels were set to $p < .05$ (FDR-corrected); cluster size: $k > 30$ voxels.

4. Results

4.1. Behavioural data

4.1.1. Response time

The auditory paradigm resulted in a significantly longer mean response time (2918ms) than the visual paradigm (2006ms). This difference was due to the self-paced nature of the visually presented sentences. Most subjects were university students and must therefore be considered highly skilled readers.

Sentences with a concrete landmark elicited slightly faster responses than those with an abstract landmark, both in the visual and in the auditory paradigm when compared by a two-sample non-parametric rank-sum test ($p < .05$) (Table 1).

The response to sentences with an animate subject noun showed a tendency to be slower than the response to sentences with inanimate subject nouns. However, the difference was not significant in the visual paradigm, and only significant in the auditory paradigm ($p < .05$) before correcting for the slightly longer duration of the inanimate sentences (Table 1).

4.1.2. Responses

Analysis of the response data demonstrated that the volunteers categorised most (79–89%) sentences of type An–Co, An–Ab, and In–Co as ‘understood’ (Table 1). Due to the semantic combinatorics of the paradigm discussed above, In–Ab sentences were expected to be difficult to interpret, and these sentences were mainly (86%) characterised as ‘not understood’ (Table 1).

4.2. fMRI data

4.2.1. Modality specific activations

Brain regions more active in the listening paradigm than in the reading paradigm were found mainly in the auditory cortices bilaterally and in the paracentral lobule (Fig. 1A). Brain regions more active in the reading paradigm than in the listening paradigm were found only in the striate and extra striate visual areas of the cerebral cortex (Fig. 1B). These findings are consistent with the expected activation patterns specific to the respective sensory modality. This supports the claim that the cross-modal analyses pursued in the following emphasise the semantic content while factoring out the sensory activation itself. It will therefore not be discussed further.

4.3. Cross modal activations

4.3.1. Main effect and interactions

We then analysed the main effects and the interactions of the two factors in the stimuli—animacy of the grammatical subject and concreteness of the preposi-

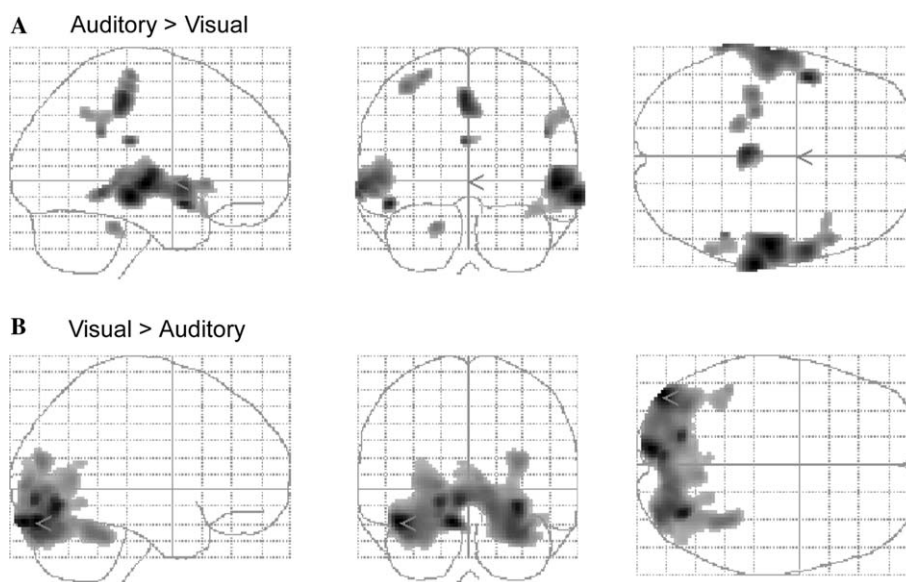


Fig. 1. Primary perceptual activations Significant activations ($p < 0.05$, FDR-corrected) from (A) auditory paradigm > visual paradigm; (B) visual paradigm > auditory paradigm. These reflect primary perceptual aspects of language processing. As expected listening to speech evokes activity in auditory cortex while reading generates activity in primary and secondary visual brain regions.

tional landmark—in the pooled data from the auditory and visual stimulations. We did not find any brain regions that were significantly activated or deactivated as a main effect of animacy ($p > .05$ FDR-corrected). This suggests that at a sentence level, animacy is not per se a good candidate for neural categorical specificity.

When compared with sentences with an abstract landmark (An–Ab and In–Ab), sentences with concrete landmarks (An–Co and In–Co) activated a number of mainly posterior brain areas, including bilateral activations of the fusiform gyri, parahippocampal gyri, retrosplenial gyri, and the occipital–temporal–parietal junction. Significant activations were also found in the left posterior cingulate (including precuneus) and in the left middle and the right medial frontal gyri (Table 2; Fig. 2).

When compared with sentences with a concrete landmark, sentences with an abstract landmark activated a mainly anterior, slightly left-lateralised network in anterior middle and superior temporal regions, including bilateral activation of the temporal pole, and frontal regions, including the inferior frontal gyri. A widespread unilateral activation of the left superior frontal gyrus was also detected. (Table 3; Fig. 3A).

We did not detect any brain regions that were significantly activated or deactivated by an interaction between animacy and concreteness.

4.3.2. Activations evoked by individual sentence types

We did not model the direct effect of the two response types (“understood”/“not understood”) due to the

Table 2

Peak coordinates for significantly activated clusters in the concrete > abstract contrast ($p < .05$, FDR-corrected)

Cluster locations	Brodman	MNI x	MNI y	MNI z	z score
<i>Concrete > abstract landmark</i>					
L fusiform & Parahippocampal gyrus	20.37	−32	−44	−20	5.35
R fusiform & Parahippocampal gyrus	20.37	30	−38	−24	4.61
L retrosplenial	30	−16	−64	8	3.01
R retrosplenial	30	14	−58	4	4.85
L occipital–temporal–parietal junction	19	42	−80	18	4.74
R occipital–temporal–parietal junction	19	−40	−82	16	4.21
L&R cingulate gyrus, R postcentral gyrus	5.31	−4	−40	40	4.83
L precuneus	7	−24	−74	38	4.29
L middle frontal gyrus	8	−32	28	44	3.35
R medial frontal gyrus	10	10	52	−12	3.67

A bilateral pattern of activations in the temporal and parietal lobes is detected, analogous to activation patterns seen following non-linguistic spatial navigation tasks.

Concrete Landmark > Abstract Landmark

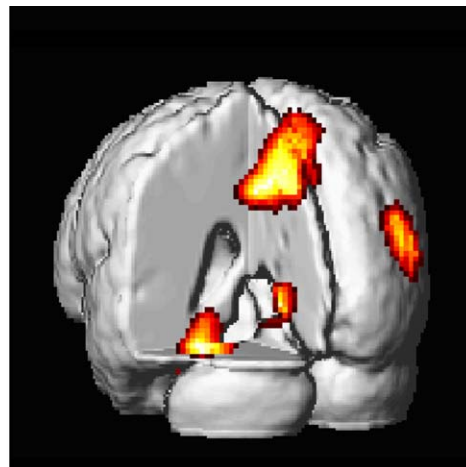
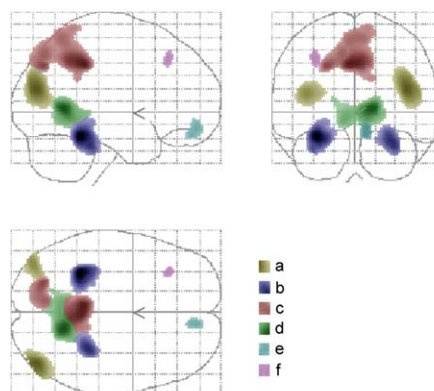


Fig. 2. Effect of concrete landmark. Left: significant activations ($p < 0.05$, FDR-corrected) from sentences with concrete landmark versus sentences with abstract. Activations are seen bilaterally in: (a) TOP-junction, (b) fusiform and parahippocampal gyri, (c) precuneus/posterior cingulate region, and (d) retrosplenial cortex. Small frontal activations are also detected in (e) left middle frontal gyrus, and (f) right medial frontal gyrus. See Table 2 for details. Right: same activations shown on a rendered normalised mean structural image of the 17 subjects. Cut surfaces in MNI coordinates are: $x = -10$, $y = -42$, and $z = -20$. This network of activations has previously been found in mental navigation tasks and in processing of images with topographical information.

Table 3

Peak coordinates for significantly activated clusters in the abstract > concrete contrast ($p < .05$, FDR-corrected)

Cluster locations	Brodman	MNI x	MNI y	MNI z	z score
<i>Abstract > concrete landmark</i>					
L inferior frontal gyrus	47	−44	38	−14	4.34
	47	−46	20	2	3.96
R inferior frontal gyrus	47	48	36	−10	3.92
	13	32	14	−14	3.12
	45	62	20	16	3.1
L superior frontal gyrus	9	−14	58	30	4.45
	9	−8	54	30	4.3
	8	−36	14	52	3.08
L middle frontal gyrus	6	−40	−2	52	3.18
R middle frontal gyrus	6	42	4	54	3.08
	10	28	42	26	3.63
L medial frontal gyrus	6	−4	0	62	4.11
L temporal pole	38	−48	18	−22	4.57
R temporal pole	38	52	16	−28	3.98
L middle temporal gyrus	21	−50	6	−36	5.48
	21	−64	−22	−12	5.29
	21	−60	−10	−16	4.86
R middle temporal gyrus	21	58	−2	−18	4.86
	21	40	2	−38	4.64
L superior temporal gyrus	39	−60	−62	18	3.12
	39	−44	−60	16	3.01
L posterior cingulate	31	−2	−56	22	3.9
Cerebellum		0	−76	−46	3.47

A large slightly left-lateralised fronto-temporal pattern of activation is seen. These areas have all previously been related to complex semantic processing, such as seen in the comprehension of narratives.

block design of the experiment. However, as seen from the response data (Table 1) more than 80% of the An–Co, An–Ab, and In–Co sentences were categorised as understandable while this was only the case for about 20% of the In–Ab sentences. As there were no significant interactions between the factors, we would therefore, expect that comparing In–Ab sentences to the three other sentence types would reveal brain regions whose activity correlated positively with the effect of not understanding a sentence. This analysis identified one area in the right inferior frontal gyrus (Fig. 3C) (x , 50; y , 42; and z , −8; z score, 5.00).

When comparing An–Ab sentences to the other three sentence types, we found a pattern of activation very similar to the one evoked as a main effect of abstract sentences, but without the right sided frontal activations and some of the right temporal activation. Interestingly, the right sided temporal pole activation is maintained (Fig. 3B). This activation pattern reflects mainly the comprehensible part of the abstract sentences. No significant activations were found when comparing either of the two concrete sentence types to the rest.

4.4. Pairwise comparison of sentence types

A pairwise comparison of sentence types within the animacy factor (An–Co versus In–Co and An–Ab versus In–Ab) did not identify any brain regions that survived our criteria of significance. However when comparing In–Co sentences with An–Co, a small activation (19 voxels) in a white matter region of the right parietal lobe (Peak MNI coordinates: x , 32; y , −62; z , 30) was just below the threshold for cluster size. Pairwise comparisons of the two animate sentences (An–Co versus An–Ab) and the two inanimate sentences (In–Co versus In–Ab) repeated the main effects, though less significant.

5. Discussion

In this study, we have investigated the neural activity underlying linguistic processing at a sentence level. The sentences presented were structurally identical but differed systematically in terms of two factors: the animacy of the grammatical subject and the con-

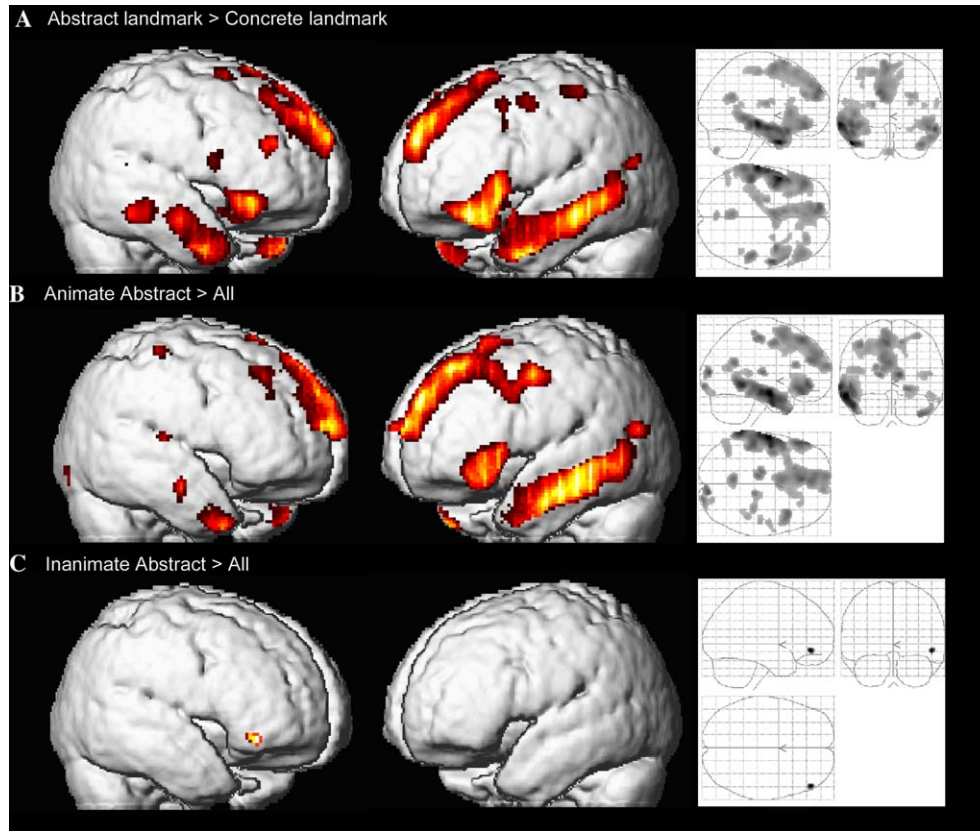


Fig. 3. Effect of abstract landmark. Significant activations ($p < 0.05$, FDR-corrected) from (A) abstract landmark > concrete landmark, (B) animate subject and abstract landmark (An–Ab) > All, and (C) In animate subject and abstract landmark (In–Ab) > All, are shown both on a 3D rendering of the mean normalised structural image from the 17 subjects and on a glass brain. As can be seen from a comparison of (A and B), most of the left lateralised activation generated by the collected abstract sentences (A) seem to stem from the An–Ab type (B) reported to be understood by the subjects, whereas the right lateralised inferior frontal activity primarily is generated by the less understandable In–Ab sentences (C). Both left inferior frontal gyrus and the temporal poles have been argued to play a role in complex semantic processing, such as narratives or “scripts.” The right inferior frontal gyrus seen activated by the odd In–Ab sentences (C) might be involved in the processing of semantic incongruity.

creteness of the prepositional noun. This suggests that the differences in brain activations across sentence types indicate differences in the neural substrates for semantic processing. There was no main effect of animacy in this study, but a number of brain areas are significantly activated as the main effect of concreteness. When designing the study, we hypothesised that sentences with concrete landmark (An–Co and In–Co) would elicit activation in brain regions involved in non-linguistic spatial processes when compared with sentences with abstract landmark. As we will discuss in details below, the brain regions activated by this contrast are, indeed, strikingly similar to those reported in non-linguistic topographical tasks, such as mental navigation (Ino et al., 2002). This supports our hypothesis. We were not able to find solid support for our second and third hypotheses that fictive motion (In–Co) and ordinary motion sentences (An–Co) would induce significant activations in brain regions responsible for allocentric and egocentric motion construction, respectively. Finally, we hypothesised that In–Ab sentences

would activate frontal regions. We found one such region in the right inferior frontal gyrus.

5.1. Activations by sentences with concrete landmark

In this study, sentences with a concrete landmark activate an extended network of brain regions including fusiform/parahippocampal gyri, retrosplenial region and temporo-occipital-parietal junction and precuneus. Brain imaging experiments have unequivocally demonstrated that these regions may be jointly activated also by non-linguistic experimental paradigms that enforce processing of topographical features. In a recent brain imaging experiment of subjects engaged in wayfinding in a virtual-reality environment Hartley, Maguire, Spiers, and Burgess (2003) identified a similar network of regions, including fusiform-, parahippocampal-, retrosplenial-, and posterior parietal cortices, the precuneus and the caudate body. In a different experiment, a memory retrieval task following virtual-reality experiences showed much the same network of temporal-parietal

activations, including the hippocampus and frontal regions, when subjects recalled spatial information (Burgess, Maguire, Spiers, & O'Keefe, 2001). A mental navigation task where subjects were asked to “move” between different known locations in the real world also activated parahippocampal and retrosplenial regions and the temporal–occipital–parietal junction (in the following abbreviated as TOP) (Ino et al., 2002). Based on the strikingly similar pattern of activity, we propose that the sentences with concrete landmark may establish in the listener an imageable mental space by activating brain regions also involved in the processing of topographical information conveyed non-linguistically. We will in the following examine this claim through a region-by-region review of studies involving topographical processing, which have activated these areas.

5.2. Fusiform/parahippocampal gyri

Using pictures as stimuli, bilateral involvement of the parahippocampal gyri has been identified when images exhibit extended spatial properties relative to single objects or faces (Epstein, DeYoe, Press, Rosen, & Kanwisher, 2001; Epstein, Graham, & Downing, 2003; Epstein, Harris, Stanley, & Kanwisher, 1999; Epstein & Kanwisher, 1998; Maguire et al., 1998; Maguire, Frith, & Cipolotti, 2001). Bar and Aminoff (2003) have argued that parahippocampal and retrosplenial regions play a role in processing images with strong contextual ties relative to images with weak context, but others have shown activation of the parahippocampal region even with subliminal presentations (Marois, Yi, & Chun, 2004).

A number of experiments examining the imageability of single nouns whether read or heard also report activation in the anterior fusiform- and parahippocampal gyri and in the hippocampus (Bartha et al., 2003; D'Esposito et al., 1997; Fletcher et al., 1995; Wise et al., 2000), though others have failed to find a difference between concrete and abstract words (Buchel, Price, & Friston, 1998).

Taken together, these findings do not provide a clear distinction between the function of the anterior part of the fusiform gyrus and the parahippocampal gyrus. Also, activity in fusiform/parahippocampal regions can not be said to reflect contextual specificity per se—at least not when processing linguistic material. Rather, it seems to reflect differential semantic processing, and it appears consistent with the reviewed literature that activity in this region occurs when the stimuli have concrete, imageable spatial properties.

5.3. Retrosplenial region

Retrosplenial activations have been reported during recall of spatial information in a virtual reality environ-

ment (Burgess et al., 2001), and in memory encoding of visual topography (Cipolotti & Maguire, 2003). Ino et al. (2002) also report a very strong retrosplenial activation in a mental navigation task. They hypothesise that this area is equivalent to area V6A in monkey, a brain region with position cells, where the receptive fields are anchored to egocentrically defined spatial coordinates. They therefore, propose that activity in this region may allow to transform a visual scene from world-centred coordinates into a self-centred perspective. Bar and Aminoff (2003) report that images with strong contextual cues evoke retrosplenial activation.

Language studies involving topographical information have also resulted in retrosplenial activations. Damasio et al. (2001) report that naming of spatial relations from images activate the retrosplenial region, along with TOP and fusiform areas.

These results support the hypothesis that the retrosplenial region is involved in the processing of spatial semantics, both linguistically and non-linguistically mediated.

5.4. TOP—temporal–occipital–parietal junction

Activations at the junction between the temporal, occipital, and parietal lobes (Brodmann 19/39), are seen in apparently very different activation paradigms such as memory encoding, image processing, language comprehension, and attentional tasks.

Experiments involving mental navigation in a known environment have shown bilateral activity at the TOP junction along with the parahippocampal gyrus and the retrosplenial region (Ino et al., 2002; Maguire, Frackowiak, & Frith, 1997). Strongly contextual images also evoke more activity in the vicinity of the TOP junction than weakly contextual images (Bar & Aminoff, 2003). A PET study of pictures with emotional content reports bilateral TOP activation when images depicting complex scenarios or “situations” are contrasted with images of faces, regardless of their emotional value (Geday, Gjedde, Boldsen, & Kupers, 2003). Similarly, TOP activations are seen when subjects make judgement about spatial properties of images (indoors/outdoors) relative to the emotional impact on the viewer (Lane, Fink, Chau, & Dolan, 1997). Memory encoding of images with a spatial content (both landscapes and buildings) have been reported to give right lateralised TOP activity relative to abstract images (Maguire et al., 2001).

These studies demonstrate that the TOP area plays a role in processing visual topographical information. TOP activations have also been seen in semantic decision tasks that require spatial imagery such as subjects reporting on the locations versus the colours of the content of written nouns (Mummery, Patterson, Hodges, & Price, 1998), and subjects reporting the size or locational origin of objects (Cappa, Perani, Schnur, Tettamanti, &

Fazio, 1998; Noppeney & Price, 2003; Scott, Leff, & Wise, 2003).

In a review, Aguirre and D'Esposito (1999) argue that lesion to the posterior parietal lobe can cause egocentric topographical disorientation, where patients are unable to represent objects with respect to themselves. Spatial imagery can also be severely impaired, resulting in neglect syndrome (Driver & Mattingley, 1998). Cooper and Humphreys (2000) report of a patient with Balint's syndrome, following bilateral temporo-parietal and right sided occipito-parietal damage, who was unable to code spatial relations between objects, but who had preserved relational coding within objects, and who was still able to read single words. It is also known, that the vestibular system for monitoring head movements projects information to the posterior parietal cortex for information processing in relation to self-motion (Andersen, Shenoy, Snyder, Bradley, & Crowell, 1999). All in all, it seems probable that the TOP junction area is involved in monitoring the relation between the subject and the external spatial environment, and, as we show, that this relationship can be linguistically encoded.

5.5. Precuneus

The existing literature clearly suggests that the areas hitherto discussed are involved in the processing of topographical information. However, the case is less clear for the posterior cingulate and precuneus activations. Virtual reality navigation studies report precuneus activations for wayfinding, both relative to route- and to trail following (Hartley et al., 2003), and recall of place in a VR environment also activates precuneus relative to recall of persons (Burgess et al., 2001). During encoding of topographical images, healthy control subjects had more activity in precuneus than a subject with semantic dementia (Cipolotti & Maguire, 2003). On the other hand, Maguire et al. find no precuneus activation in subjects encoding topographical images, while encoding images of faces appears to activate this region (Maguire et al., 2001). Kosslyn et al. have shown precuneus involvement in top down perception and in imagery tasks (Kosslyn, Thompson, & Alpert, 1997), while an early PET study showed a clear precuneus activation as a function of word imageability (Fletcher et al., 1995). Finally, the region appears to be involved in maintenance of self-awareness (Kjaer, Nowak, & Lou, 2002).

5.6. Bilateral activations

Single word studies often find only left lateralised inferior temporal activations (Buchel et al., 1998; D'Esposito et al., 1997; Wise et al., 2000). This is in line with an understanding of the brain, where the left hemi-

sphere is considered to be most important for solving linguistic tasks, whereas spatial tasks are associated mainly with the right hemisphere, though less pronounced in women (Toga & Thompson, 2003; Vogel, Bowers, & Vogel, 2003).

In this study, sentences with an abstract landmark, which did not provide an imageable topography, activated mainly 'classic' left lateralised temporal language areas, while concrete sentences caused an almost symmetrical mainly bilateral and posterior pattern of activity. The concrete sentences were constructed to evoke contextual meanings, which unfold multi-dimensional mental spaces that involve both linguistic and topographical elements. We find it likely that the bilateral pattern of activity reflects that understanding these sentences requires the joint activity of 'linguistic' and 'topographic' brain regions. However, it can not be ruled out that the left lateralised pattern of activity found in most single word experiments is an experimental artefact caused by a low statistical power. The most comprehensive brain imaging study of semantic word processing (including 70 subjects) also report bilateral activations in the inferior temporal region, but unfortunately no information is provided from other parts of the brain (Bartha et al., 2003).

5.7. No hippocampus activation

As discussed above, studies of mental navigation have identified a network of brain regions very similar to the one caused by concrete landmark sentences. In addition, some of these studies have also found significant activations in the hippocampus (Burgess et al., 2001; Hartley et al., 2003). We did not find activation of the hippocampus proper. However, this is not surprising. The hippocampus is known to play a role in navigation and memory (Burgess, Maguire, & O'Keefe, 2002; O'Keefe & Nadel, 1978), and due to the generic nature of the nouns used in our experiment (e.g., "the man," "the house," etc.), neither explicit memory retrieval nor memory encoding is needed. Further, any hippocampal activation related to semantic retrieval, would be equally distributed in the concrete landmark and abstract landmark conditions and hence factor out in the analysis.

5.8. Abstract landmark

The areas activated as a main effect of abstract landmark, including the middle and superior temporal cortices bilaterally and the inferior frontal cortex bilaterally, have all been found in studies related to complex semantic reasoning (Fiez, 1997; Maguire, Frith, & Morris, 1999; Price, 2000; Scott et al., 2003), including categorisation of artefacts (Grabowski, Damasio, & Damasio, 1998; Martin, Wiggs, Ungerleider, & Haxby, 1996; Pera-

ni et al., 1995). To our knowledge, none of these regions have previously been identified with spatial processing. This suggests that when the simple spatial schema supplied by the preposition is applied to an abstract complement noun, a complex “script” emerges. As a result the spatial meaning potentially provided by the preposition is transformed into an aspectual meaning. This does not directly evoke a concrete imageable mental space, but it rather takes the form of a narrative or a metaphor. However, due to the factorial design it can not be ruled out that the abstract landmark sentences would have generated activation in topographical brain regions relative to a hypothetical low-level baseline.

Analysis of the activations evoked by An–Ab and In–Ab sentences, respectively, indicate that most of the left lateralised activity seen in the main effect appears to have been driven by An–Ab sentences. Indeed, the processing of these sentences with an animate subject and an abstract landmark appears to rely on a distinct temporal and prefrontal network of mainly left lateralised brain regions comprising a number of regions involved in the understanding of narratives (Maguire et al., 1999) (Fig. 3). As discussed above, we find it likely that the distinct activation in the right prefrontal cortex associated with the processing of In–Ab sentences reflect that most of these were evaluated as ‘not understandable.’

Differences in sentence difficulty could also, at least partly, explain the greater temporo-frontal activations seen with the abstract sentences. Subjects generally used more time to react to the abstract sentences than the concrete sentences (Table 1). Further studies, perhaps including additional stimulus categories, are needed to clarify what a putative relationship between cognitive “effort” and the experience of meaning would be in neural terms.

5.9. No animate/inanimate distinction

We found no main effect activation related to animacy and inanimacy. This suggests that—at least at the level of sentences—this contrast is not an unequivocal marker of differential brain activity. The distinction between animate and inanimate nouns has been a key category in feature based theories of semantics (Warrington & McCarthy, 1987; Warrington & Shallice, 1984) but earlier brain imaging studies designed around this contrast have generated contradicting and inconclusive results (Devlin et al., 2002). We take this to indicate that a feature based theory of semantics must take into account contextual considerations. Such have, however, often been left implicit both in functional imaging experiments and in the clinical practice, although recently the existence of “a spatial code” in conceptual knowledge has been proposed (Crutch & Warrington, 2003).

5.10. No specific effect of “fictive motion”

We hypothesised that fictive motion sentences (In–Co) would yield activity in brain regions responsible for egocentric motion construction relative to ordinary motion sentences (An–Co), which was thought to involve primarily allocentric motion construction. We were not able to substantiate this claim in the current experiment. We detected a small right lateralised activation in the parietal lobe, but this fell under our threshold for activation cluster size and was situated deep in white matter. Further investigation might clarify if this was relevant. Alternatively, in spite of the apparent differences at a linguistic level allocentric and egocentric motion constructions might turn out to be complementary, possibly indistinguishable cognitive functions at a neuronal level.

6. Conclusions

This study demonstrates that concrete imageable mental spaces produced with verbal cues unfold via the same brain regions involved in processing topographical information by other cognitive modalities. This supports an “overlapping systems” view of language (Talmy, 2000) in which the processing of spatial semantics is a special case of more general cognitive processing.

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Appendix

Examples of sentences used both in the visual and auditory paradigm.

An–Co sentences

Manden går gennem dalen
 Munken går ind i labyrinten
 Patienten går ind i gipsvæggen
 Studenten løber gennem bygningen
 Manden kommer fra landsbyen
 Trommeslageren kommer ind i landet
 Pigen løber rundt om bymidten
 Rengøringsdamen begynder ved spisebordet
 Detektiven når ind til slottet
 Hunden dukker op i horisonten

An–Ab sentences

Manden går gennem livet
 Munken går ind i bønnen
 Patienten går ind i sindssygen
 Studenten løber gennem uddannelsen
 Manden kommer fra socialvæsenet
 Trommeslageren kommer ind i rytmen
 Pigen løber rundt om problemet
 Rengøringsdamen begynder ved begyndelsen
 Detektiven når ind til svaret
 Hunden dukker op i historien

In–Co sentences

Hegnet går gennem dalen
 Snoren går ind i labyrinten
 Messingskrueen går ind i gipsvæggen
 Ledningen løber gennem bygningen
 Grusvejen kommer fra landsbyen
 Olieledningen kommer ind i landet
 Ringvejen løber rundt om bymidten
 Blodsporet begynder ved spisebordet
 Allé en når ind til slottet
 Kirken dukker op i horisonten

In–Ab sentences

*Hegnet går gennem livet
 *Snoren går ind i bønnen
 *Messingskrueen går ind i sindssygen
 *Ledningen løber gennem uddannelsen
 *Grusvejen kommer fra socialvæsenet
 *Olieledningen kommer ind i rytmen
 *Ringvejen løber rundt om problemet
 *Blodsporet begynder ved begyndelsen
 *Alléen når ind til svaret
 Kirken dukker op i historien

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