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Neuronal activation for semantically reversible sentences

Fiona M.Richardson[1, 2], Michael S.C. Thomas[1] & Cathy J. Price[2]

1. Developmental Neurocognition Lab, School of Psychology, Birkbeck College, University of London.
2. Wellcome Trust Centre for Neuroimaging, University College London.

Address for correspondence:
Dr. Fiona Richardson
Wellcome Trust Centre for Neuroimaging, UCL
12 Queen Square
London
WC1N 3BG
Email: fiona.richardson@ucl.ac.uk
Tel.: +44 (0)20 7833 7488
Fax: +44 (0)20 7813 1420

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Abstract

Semantically reversible sentences are prone to misinterpretation and take longer for typically developing children and adults to comprehend; they are also particularly problematic for those with language difficulties such as aphasia or Specific Language Impairment. In our study we used functional magnetic resonance imaging (fMRI) to compare the processing of semantically reversible and non-reversible sentences in 41 healthy participants in order to identify how semantic reversibility influences neuronal activation. By including several linguistic and non-linguistic conditions within our paradigm, we were also able to test whether the processing of semantically reversible sentences places additional load on sentence-specific processing, such as syntactic processing and syntactic-semantic integration, or on phonological working memory. Our results identified increased activation for reversible sentences in a region on the left temporal-parietal boundary, which was also activated when the same group of participants carried out an articulation task which involved saying "one, three" repeatedly. We conclude that the processing of semantically reversible sentences places additional demands on the sub-articulation component of phonological working memory.

Introduction

Some sentences are harder to process than others. Whilst the overall complexity of a sentence may be modulated in terms of its grammatical structure, there are additional properties which can increase sentence complexity. A prominent class of such sentence types are semantically reversible sentences (e.g., "*The leopard races the young lion"* see Figure 1). These sentences have an interesting property in that when the subject (e.g. *leopard*) and the object (e.g. *lion*) are swapped or *reversed* (e.g., "*The lion races the young leopard")*, these sentences remain meaningful, although the exact meaning of the sentence is changed (for instance the animal doing the *racing* changes). By contrast, in a non-reversible sentence (e.g., *"The dog chews the bone"* see Figure 1) swapping the subject (e.g. *dog*) and the object (e.g. *bone*) results in a sentence with no real meaning (*"The bone chews the dog"*).

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Insert Figure 1 about here
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Both typically developing children and adults alike take longer to comprehend semantically reversible sentences, which are also more prone to misinterpretation than non-reversible sentences (Herriot, 1969; Kemper & Catlin, 1979; Slobin, 1966; Turner & Rometveit, 1969). This added difficulty may be attributed to a reduction in the constraints on (theta) role assignment of the *subject* and *object* for reversible sentences. Reversible sentences can become even more difficult to interpret when their grammatical structure deviates from the subject-verb-object word order typically found in English. For instance, reversible passives (e.g., *"the dog was bitten by the fox"*) are consistently misinterpreted by typical adults across a range of sentence types (Ferreira, 2003). An explanation for this extra complexity is that individuals cannot rely on a simple word order heuristic for role-assignment. In some instances it may prove useful to assess the semantic likelihood of events occurring in the sentence referenced by the verb (for example, it is more likely that a *cat* would be *chasing* a *mouse* than vice versa) but this may also lead to misinterpretation. Thus, consistently correct interpretation of reversible sentences is dependent on a full evaluation of syntactic structure, a property which makes these sentences particularly important in the assessment of syntactic processing capabilities. For instance, semantically reversible sentences are used to determine the preservation of syntactic processing skills in acquired and developmental disorders of language, such as "agrammatic" aphasia and SLI, as well as degenerative disorders such as Alzheimer's disease (Bickel, et al., 2000; Waters & Rochon, 1998). However, there is some debate as to whether difficulty in processing semantically reversible sentences is purely indicative of a syntactic deficit, or whether difficulties in processing these sentences arise from other sources.

The account that difficulty in processing reversible sentences is indicative of a syntactic deficit was put forward by Caramazza and Zuriff (1976), who found that "agrammatic" Broca's aphasics struggle to comprehend reversible sentences. They argued that agrammatic aphasics are unable to evaluate syntactic structures, and must therefore rely upon simple heuristic strategies for sentence comprehension which are prone to failure. Grodzinsky (1990) explained the sentence processing difficulties of Broca's aphasics in terms of damage to a specific sentence processing mechanism that connects an antecedent with its trace. Processing semantically reversible sentences is also particularly problematic for young children with Specific Language Impairment (SLI), which is a developmental disorder of language occurring in the absence of cognitive impairment or brain damage (Leonard, 1988). Grammar-specific accounts of this disorder are also a prevalent feature of the literature (van der Lely 2000; van der Lely & Christian, 2005; van der Lely & Stollwerk, 1996; Rice, 2000). However, there is no consensus view. Indeed, there is considerable debate as to whether the cause is specific to grammar in both the SLI (Gathercole & Baddeley, 1990; Ullman & Pierpoint, 2005) and the aphasia literature (Berndt et al., 1996; Grodzinsky et al., 1999).

A second explanation for the sentence processing difficulties of Broca's aphasics emphasises the role of semantic processing in sentence comprehension, suggesting that their difficulty in understanding sentences arises from an inability to integrate the syntactic structure of a sentence with semantic information (Saffran et al., 1998; Berndt, et al., 2004). A third alternative proposes that the deficit lies in phonology. For instance, Gathercole & Baddeley (1990) argue that phonological problems are the principal cause of SLI, pointing to data which indicates that children with SLI have a reduced phonological working memory capacity in comparison to both their age-matched peers and language-matched control participants (Gathercole & Baddeley, 1990; Mongomery, 1995a; 1995b, 2004; Dollaghan & Campbell, 1998; Ellis Weismer et al., 2000). A fourth perspective is that reduced capacity across the whole sentence processing network will have a greater detriment on semantically reversible sentences (Caplan et al., 2007).

In summary, semantic reversibility increases the processing difficulty of a sentence across a range of grammatical constructions. Moreover, these sentences are particularly vulnerable in both developmental and acquired disorders of language. The present study aims to identify brain regions associated with the processing of semantically reversible sentences over a range of sentences with different syntactic structures, thus examining the overall property of semantic reversibility on sentence processing. We compared the processing of semantically reversible versus non-reversible sentences in auditory and visual processing modalities in normal individuals with no history of developmental or acquired language difficulties. The inclusion of both modalities allowed us to focus on amodal sentence processing, rather than modality-specific effects. Our paradigm also included additional linguistic and non-linguistic tasks that allowed us to functionally localize systems that were differentially responsive to the syntactic and semantic demands of sentence level or articulatory processing. This allowed us to determine whether the functions of the brain regions associated with semantically reversible sentences are most consistent with syntactic/syntactic-semantic processing, phonological processing, amodal semantics, or all of the above, (for further details see the experimental paradigm section). Moreover, by deliberately including a large sample of participants (47) with a wide age range (7 to 73 years) and verbal ability range, we were able to test whether the effect of reversible relative to non-reversible sentences was dependent on level of vocabulary knowledge, memory, age and general cognitive ability.

Materials and Methods

Participants

The participants were 47 right-handed volunteers (24 males) aged between 7 and 73 years, who had English as their first language. All participants had normal or normal-corrected vision, with no reported hearing difficulties or disturbances in speech comprehension, speech production, or reading. Six participants were excluded due to an incomplete coverage of temporal brain regions in the functional scans (remaining total of 41 participants). This study was approved by the joint ethical committee of the Institute of Neurology and the National Hospital for Neurology and Neurosurgery, London, UK. Informed consent (written consent from a parent or guardian in the case of young children under 16) was obtained from all participants.

Behavioural tests

All participants carried out two psychometric tests: (i) the British Picture Vocabulary Scales II (BPVS II – Dunn et al., 1997), and (ii) the Matrices task from the British Ability Scale II (BAS II – Elliot et al., 1997). All participants between 7 and 11 years also carried out the Reading test from the BAS-II to ensure that they had sufficient reading ability to carry out the functional imaging paradigm. The reading test consists of ninety words divided into nine blocks of ten words. Children start the test at an age appropriate starting point and read aloud a series of words presented on a card. The words increase in complexity as the test progresses. The test is continued until the child makes eight or more consecutive errors. An ability score that takes into account the difficulty of the test items completed is then obtained using a look-up table supplied with the test. Children with a minimum reading age of seven years were considered to be at an appropriate level to carry out the reading task used in the fMRI paradigm given that the sentence stimuli were designed to be suitable for children of this age (for further details, see section on sentence stimuli). All children who took part in this study had a reading level in line with or in advance of their chronological age (reading age range of 7 years and 4 months to 15 years and 3 months). Therefore, although older participants were expected to be more proficient readers, the younger children included in this study were capable of comprehending the sentence stimuli.

The BPVS-II is a measure of an individual's receptive vocabulary for Standard English. In this test, participants are asked to select (from four options) the picture that most accurately matches a word (such as *"ladder",* or *"collision"*) read aloud by the tester. The test consists of fourteen sets of words of increasing levels of difficulty, each containing twelve items. Each set has an approximate age-range indicator, which is used to select the appropriate starting set. Providing the performance of the participant meets the criterion of one or no errors on this initial set, the *base* set is established (should the participant make more than one error, preceding sets are administered until a base set is determined). The test is then conducted until the participant makes eight or more incorrect responses within a set (the *ceiling* set). The raw test score is calculated by taking the item number of the ceiling set and subtracting from it the total errors made over all sets from the *base* set onwards.

The Matrices task from the BAS-II was used as a measure of general cognitive ability. In this test, participants are shown an incomplete matrix of black and white abstract figures, with each matrix consisting of either four or nine cells. Participants are required to select the most appropriate pattern to complete the matrix from six potential tiles by pointing to or reading the number of the tile that best completes the matrix. Participants first complete four practice items, and then begin the test at an age-appropriate level, which is indicated on the test (previous items are administered should they fail on the first three test items). The test is discontinued if the participant makes five failures out of six consecutive items. An ability score, which takes into account the number and level of difficulty of the test items completed, is then obtained from a look-up table supplied with the test.

Experimental paradigm

The experimental paradigm consisted of four activation tasks: (1) auditory sentence processing, (2) visual sentence processing, (3) hand action retrieval in response to pictures of familiar objects, and (4) articulation. Details of these activation conditions and their corresponding baselines are provided below. In brief, auditory and visual sentences were either reversible or non-reversible. Direct comparison of these sentence types identified regions associated with reversible sentence processing. To assign a functional role to the areas associated with reversible sentences we considered the previous literature and also the pattern of activation across a range of tasks in our own subjects. S*yntactic and syntactic-semantic* areas were expected to be included in the set of areas activated for both auditory and visual sentence processing over and above all other conditions. Likewise, *articulatory* areas were expected to be included in the set of areas activated for the articulation task over and above all other conditions. We also identified *amodal semantic* areas as those that were activated for auditory sentences, visual sentences, and hand action retrieval in response to pictures of objects. An important point to note here, prior to describing the conditions in detail, is that our experimental design and the interpretation of our data were not based solely on subtractive logic. Thus, we acknowledge that the comparison of auditory and visual sentences to all other conditions will include processes other than syntactic-semantic processing (e.g. working memory). The interpretation of our results therefore rests on the integration of our findings with those in the previous literature. The inclusion of multiple conditions in the present design has two strong advantages over the previous literature: (1) it avoids the well-known pitfalls of reverse inference (problems with deductive validity; see Poldrack, 2006); and (2) it tests whether a novel effect (reversible sentences versus non-reversible sentences) overlaps with activation for other conditions within the same subjects. In other words, by including multiple conditions, we provide our own subject-specific localizers.

Auditory and visual sentence processing: participants listened passively to auditory sentence stimuli, and silently read visual sentences. These activation tasks consisted of three types of sentence stimuli: (i) reversible sentences, (ii) non-reversible sentences, and (iii) scrambled sentences (strings of words that did not constitute a meaningful sentence). The baseline task in the auditory modality consisted of listening to the same speech recordings after they had been rendered meaningless by digital reversal. In the visual modality the baseline task consisted of viewing the same words presented in an unrecognisable (false) font.

We chose passive listening/reading tasks for three reasons. First, they have the advantage of avoiding task-induced strategies over and above the speech comprehension processes that we were interested in. Second, they allow us to test the effect of reversible versus non-reversible sentences under the same conditions as behavioural studies that have demonstrated misinterpretation of reversible sentences in adults and children (Ferreira, 2003; Herriot, 1969; Kemper & Catlin, 1979; Slobin, 1966; Turner & Rometveit, 1969). Third, they do not confound sentence level processing with activation related to the production of a motor response. Although passive paradigms make it difficult to assess what the subject is doing in the scanner because there is no in-scanner behavioural measure, a significant effect of reversible versus non-reversible sentences would indicate active on-line sentence processing. Moreover, we also used an on-line video system and eye tracking to ensure that all participants were attending to the stimuli. Post-scanning memory tests (that the participants were not expecting) also ensured that the sentences had been processed because it was not possible to perform above chance on the memory test unless the sentences had been processed at the semantic and syntactic level (see below for more details).

Sentence stimuli

Sentence stimuli consisted of 40 semantically reversible and 40 non-reversible sentences with 6-8 words per sentence. Familiar words were selected to be suitable for children as young as seven years. Sentences were constructed using high frequency (>20 per million) monosyllabic and bisyllabic nouns, verbs and adjectives, and had a Flesch-Kincaid grade level readability score of 1.3. Reversible and non-reversible sentences were matched for the number of words, letters, syllables and phonemes in a sentence, as well as the mean imageability of content words, mean age of acquisition, and Kucera-Francis frequency of content words, based on information from the MRC Psycholinguistics database (http://www.psy.uwa.edu.au/mrcdatabase/uwa_mrc.htm). Both reversible and non-reversible sentence sets consisted of: active, passive, subject-cleft, object-cleft, locative and dative sentence types (these stimuli are in line with those used to identify language deficits in acquired and developmental disorders). Sentences were tested across this range of grammatical constructions in order to ensure that activations elicited during the processing of reversible sentence types could be attributed to the general property of sentence reversibility rather than a specific syntactic construction per se. These same sentence types were presented across both visual and auditory modalities to ensure consistency across tasks. Examples of sentence stimuli with further details regarding the composition of the stimuli can be seen in Table 1. Reversible and non-reversible sentence sets were each split into two groups (A and B) of equivalent composition, for the purpose of presenting one set in an auditory and the other in a visual format. No sentence was repeated across modality. The presentation of subsets A and B in either an auditory or visual format was counterbalanced across participants. Scrambled sentences were constructed from the same set of words as reversible and non-reversible sentences, consisting of initially grammatical sentences (e.g. *"The cow chased the fat horse"),* which were then assigned a pseudo-random word order that did not form a meaningful sentence (e.g. *"Chased the the horse cow fat"*). This condition is therefore fully matched to the sentences at the lexical level.

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Articulation task: Participants read aloud the visually presented digits '1' and '3' alternately. These digits were chosen because saying "one" involves pursing the lips and saying "three" involves the tongue protruding. Therefore, alternating between 1 and 3 maximised the use of the major articulators and the repetitive pattern may activate the articulatory loop component of phonological working memory. To reduce susceptibility artefacts induced by air flow during speech production and to minimise auditory processing of the spoken response, participants were instructed to make the appropriate mouth movements with minimal voicing. Responses were recorded using a specialised microphone that cancelled out the scanner noise. The baseline task consisted of making alternate mouth movements (of either pursed lips, or separated lips with the tongue slightly protruding) when prompted by a greyscale image of the desired mouth-shape displayed on-screen. We were able to distinguish which movement the participants were making using our online microphone.

Object actions task: participants viewed pictures of objects that had strongly associated hand actions, e.g., *scissors, spoon* and *calculator*. They were instructed to make the corresponding action with their right hand. In the baseline task, participants viewed pictures of objects or non-objects that did not have a strongly associated hand action and were instructed to make a rocking motion with their right hand in response to viewing the picture. To remind participants what to do in the baseline task, a red rainbow-shaped bi-directional arrow was presented above each baseline stimulus. Examples of the stimuli are shown in Figure 2. All responses in this condition were recorded using a video camera, directed on the right hand of the participant in the scanner.

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Insert Figure 2 about here
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Condition order was blocked. There were 96 blocks in total, 12 for each of the activation and baseline conditions. All 96 blocks were presented across four different scanning sessions (runs), with 24 blocks in each session. The 12 blocks of auditory sentences were subdivided into 4 blocks of reversible sentences, 4 blocks of non-reversible sentences and 4 blocks of scrambled sentences. The 12 blocks of visual sentences were subdivided in the same way. Within a session, there were 3 blocks of each activation condition and 3 blocks of baseline condition. For the auditory and visual blocks, there was one block of each sentence type (reversible, non-reversible and scrambled). This design is depicted in Figure 3.Within an 18 second block, there were: 5 sentences comprising 37 words or 37 of the corresponding baseline stimuli; 18 digits in articulation blocks or 18 images in the corresponding baseline condition; and 15 pictures in hand action retrieval blocks and the corresponding baselines. Although the total number of stimuli varied in the sentence and hand action conditions (in order to optimise processing time), this stimulus difference was removed by including the baseline stimuli (e.g. sentences – baseline versus hand action retrieval – baseline).

Each sentence, digit or picture was modelled as a separate event within condition. Therefore over sessions there were a total of 18 x 12 = 216 digit events, 15 x 12 = 180 picture events and 37 x 4 = 148 word events per sentence type. A block of an activation condition was always followed or preceded by a block of its corresponding baseline condition. Short blocks and event-related analyses were used in order to maximise experimental efficiency (Mechelli et al., 2003a; 2003b). The order of the activation conditions was counterbalanced within and between session and subject.

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Insert Figure 3 about here
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Procedure

A summary of the procedure is detailed in Figure 4, showing the presentation and timing of the stimuli across all tasks.

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Each session commenced with a visual cue to 'Get Ready…' followed by a count down, during which dummy scans were acquired. Each type of task (activation and baseline) was preceded by an appropriate visually displayed instruction (Helvetica, size 80): 'Listen' (auditory comprehension task), 'Read' (visual comprehension task), 'Mouth movements', or 'Hand movements'. This instruction was displayed for 2.2s, and was followed by an auditory pure tone, which sounded for 0.3s. Each activation and baseline task had a total duration of 18s. The presentation of activation and baseline tasks was separated by a brief auditory pure tone which sounded for 0.3s, followed by a 0.2s fixation cross. At the end of each activation and baseline task there was a 1.5s pause before the onset of the next task. This resulted in a total duration of 40.5s for an activation and baseline pair.

In the visual sentence processing task, a total of 5 sentences were presented per activation task. Each set of sentences consisted of one of each of the following sentence types: 1 active (6 words), 1 passive (8 words), 1 subject-cleft (8 words), 1 object-cleft (8 words), 1 locative/dative (7 words). Further details of these sentence types are shown in Table 1. A total of 37 words were presented in each sentence condition. Each word within each sentence was presented on-screen at a rate of one word every 0.4 seconds, (resulting in a maximum duration of 3.2s for an eight word sentence). Each word was presented in a Helvetica font size 20. Each sentence was separated by 0.5s. The auditory and visual word presentation rates were equated by recording the auditory stimuli from a female reading aloud the visual stimuli presented using the same script that was to be used in the scanner. Words were read with a flat intonation contour, minimising effects of sentence prosody in the auditory condition. Sentence change was indicated by an auditory beep, while in the visual condition the first word of each sentence started with a capital letter.

In the articulation task there were 18 presentations of stimuli per activation and baseline condition, which were displayed for 0.5s, and separated by an ISI of 0.5s. In the object action retrieval task, there were 15 presentations of stimuli per activation and baseline condition, each with an event duration of 0.5s and an ISI of 0.7s. The presentation of stimuli was set at this rate in order to limit object naming and to allow participants to complete their hand action before the onset of the next stimulus.

Memory tests

All participants carried out two pen and paper memory tests following scanning, (i) memory for sentences, and (ii) memory for pictures. Participants were not informed of these tests prior to scanning. These tasks were used to ensure that participants had been attending to the stimuli whilst in the scanner and to determine whether memory for sentences had any effect on the processing of semantically reversible sentences. The memory for sentences test consisted of 24 sentences, 12 familiar sentences (6 presented in each modality – auditory and visual) and 12 previously unseen during scanning (6 using previously presented words, and 6 using novel words). The picture memory test followed the same format, consisting of 24 names of animals and objects, 12 familiar and 12 previously unseen. All participants scored above chance on both of these tests (sentence memory test score, M = 70%, SD ± 11; picture memory test score, M = 68%, SD ± 10). The scores for the memory-for-sentences test were adjusted to account for incorrect as well as correct responses. This was done by subtracting the total of false positive responses made from the total correct responses for familiar sentences. Analyses of variance were then used to assess whether there were any differences in (i) memory for sentences according to processing modality (auditory vs. visual), and (ii) sentence type (reversible vs. non-reversible). Group (children and teenagers vs. adults) was entered as a between subject factor to test for any potential age-related behavioural differences in performance. We did not detect any main effect of sentence processing modality [$F(1, 39) = 2.06$, $p = 0.16$] or sentence type [$F(1, 39) = 0.22$, $p = 0.64$] or any interaction of group with sentence processing modality [$F(1, 39) = 0.08$, $p = 0.78$] or sentence type [$F(1, 39) = 1.18$, $p = 0.28$]. These results indicate that: (i) there were no observable effects of processing modality or sentence type on memory-for-sentences, and that there were no significant differences in these scores between children and adults. However, in order to account for individual differences in sentence memory, adjusted scores for auditory and visual memory-for-sentences were entered into subsequent analyses in SPM.

fMRI Data Acquisition

A Siemans 1.5T Sonata scanner was used to acquire a total of 768 T_2*- weighted echoplanar images with BOLD contrast (192 scans per 4 sessions). Each echoplanar image comprised 30 axial slices of 2mm thickness with 1mm inter-slice interval and 3 x 3 mm in-plane resolution. Volumes were acquired with an effective repetition time (TR) of 2.7s/volume and the first six (dummy) volumes of each run were discarded in order to allow for T1 equilibration effects. In addition, a T1-weighted anatomical volume image was acquired from all participants to ensure that there were no anatomical abnormalities.

fMRI Data Analysis

Pre-processing was conducted using statistical parametric mapping (SPM2 , Wellcome Trust Centre for Neuroimaging, London, UK; http://www.fil.ion.ucl.ac.uk/spm) running under Matlab 6.5.1 (Mathworks Inc. Sherbon MA, USA). All volumes (excluding dummy scans) from each participant were realigned using the first as a reference image and unwarped (Jesper et al., 2001), adjusting for residual motion-related signal changes. The functional images were then spatially normalised (Friston et al., 1995a) to a standard MNI-305 template using non-linear basis functions. Functional data were spatially smoothed with a 6mm full-width half-maximum isotrophic Gaussian kernel to compensate for residual variability after spatial normalisation and to permit application of Gaussian random-field theory for corrected statistical inference (Friston et al., 1995b).

First level Statistical Analysis

For each participant, data were analysed in SPM2 with high-pass filtering using a set of discrete cosine basis functions with a cut-off period of 128 seconds. Each stimulus (sentence, digit, picture, instruction etc.) was modelled as a separate event within each condition and convolved with a canonical hemodynamic response function (HRF). This resulted in 13 different conditions at the first level, which were as follows:

A) Auditory sentences: reversible

B) " " : non-reversible

C) " " : scrambled

D) " " : baseline (reversed speech)

E) Visual sentences: reversible

F) " " : non-reversible

G) " " : scrambled

H) " " : baseline (false font)

I) Hand action retrieval

J) Hand action baseline

K) Articulation

L) Mouth movements

M) Instructions

For each participant, the following 13 contrasts were generated at the first level:

1) Reversibility effect - auditory: [reversible] – [non-reversible] (= A – B)
2) Reversibility effect - visual: [reversible] – [non-reversible] (= E – F)
3) Auditory reversible sentences: [reversible] – [baseline] (= A – D)
4) Auditory non-reversible sentences: [non-reversible] – [baseline] (= B – D)

5) Visual reversible sentences: [reversible] – [baseline] (= E – H)

6) Visual non-reversible sentences: [non-reversible] – [baseline] (= F – H)

7) Auditory sentences: [sentences] – [baseline] (= A + B – 2D)

8) Visual sentences: [sentences] – [baseline] (= E + F – 2H)

9) Auditory words: [scrambled sentences] – [baseline] (= C – D)

10) Visual words: [scrambled sentences] – [baseline] (= G – H)

11) Hand action retrieval – hand action baseline (= I – J)

12) Articulation – hand action baseline (= K– J)

13) Mouth movements – hand action baseline (= L– J)

Second level Statistical Analyses

There were three different statistical models at the second (group) level.

Analysis 1: The effect of reversible > non-reversible sentences across all participants.

To identify areas that were more activated by reversible than non-reversible sentences over and above all other variables, we used a two-sample T-test with 6 covariates (in SPM5). The two samples included the contrast images from each of the 41 participants for: (1) auditory reversible sentences relative to auditory non-reversible sentences, and (2) visual reversible sentences relative to visual non-reversible sentences. The six covariates were test scores from the following cognitive measures: vocabulary knowledge (raw scores from the BPVS –II), non-verbal problem solving ability (ability scores from the BAS-II: matrices), scores for auditory memory and visual memory for sentences (derived from scores on the sentence memory test carried out after scanning), and age in months (linear, and non-linear).

The purpose of including the covariates was two-fold. First it allowed us to identify the main effect of reversible versus non-reversible sentences after potential variance from all the covariates had been factored out. Second, it enabled us to determine whether the effect of reversible versus non-reversible sentences was dependent on age, or any of the cognitive measures. The combined analysis of child and adult data is valid upon the basis of previous methodological study (Kang et al., 2003). However, in order to ensure that we had not missed any effects of reversible versus non-reversible sentences that were specific to age group, we repeated the analysis (2 sample t-test with 4 covariates: vocabulary, matrices, and auditory and visual memory for sentences) with children and teenagers only (21 participants, 10 males; mean age 14 years, range 7-17 years), and adults only (20 participants, 9 males; mean age 43.6 years, range 24-73 years).

The statistical threshold was set at $p < 0.05$ after correcting for multiple comparisons across the whole brain in either height (family wise correction) or extent. Within these regions, we also looked for the effect of covariates at $p<0.05$ uncorrected.

Analysis 2: Reversible and non-reversible sentences in children and adults

In order to examine the pattern of activation for reversible and non-reversible sentences in more detail we carried out an ANOVA in order to plot the activation for reversible and non-reversible sentences separately according to processing modality (auditory vs. visual) and age group (children and teenagers vs. adults). The following four contrast images were entered into this analysis for each age group: (1) auditory reversible sentences – baseline, (2) auditory non-reversible sentences – baseline, (3) visual reversible sentences – baseline, (4) visual non-reversible sentences – baseline. This analysis also included two covariates, which were auditory and visual memory-for-sentences. The inclusion of these scores allowed us to control for any individual differences in sentence memory test scores.

Group Level Analysis 3: Functional localizers at the group level.

The aim of this analysis was to establish whether any activation elicited for semantically reversible sentences over non-reversible sentences could be attributed to the syntactic and semantic demands of sentence processing or to articulatory processes used to index phonological working memory. To dissociate these different processing networks, and to additionally identify regions associated with amodal semantic processing, we entered contrasts (7 to 13) from the first level analysis into a second level ANOVA in SPM5.

- Sentence specific processing areas were identified as those activated by (a) auditory and visual sentences only and (b) auditory and visual sentences relative to all other conditions.
- Articulatory areas were identified as those activated by (a) the articulation task and (b) the articulation task relative to all other conditions. This combination of conditions identified regions most strongly engaged in the articulatory process (as all other conditions did not require an articulatory response), whilst also including areas that may be engaged in both articulation and sentence processing.
- Amodal semantic processing areas were identified as those activated by (a) [auditory sentences relative to baseline] + [visual sentences relative to baseline] + [hand action retrieval relative to baseline] and (b) each of the same contrasts individually. The combination of these conditions included regions that represent a common semantic system across tasks (Vandenberghe et al., 1996).

The statistical threshold for each main effect (a) was set at $p < 0.05$ after correcting for multiple comparisons across the whole brain in either height (family wise correction) or extent. In these regions with significant main effects, we report the effect of (b) at $p<0.001$ uncorrected.

Results

fMRI

Analysis 1: The effect of reversible > non-reversible sentences across all participants.

When age and cognitive ability were factored out, reversible compared to non-reversible visual sentences activated a region in the left temporal-parietal boundary, as shown in Figure 5(a). This activation bridged a lateral region of the left posterior superior temporal gyrus and the neighbouring inferior parietal region (see Table 2 for co-ordinates). We will henceforth refer to it as the left T-P region. As shown in Table 2, there was a corresponding trend for auditory reversible versus non-reversible sentences ($p= 0.003$ uncorrected) but there was also an interaction of stimulus modality with [reversible vs. non-reversible] ($Z = 3.1$, $p < 0.001$) indicating that the effect was stronger for visual than auditory sentences.

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Insert Table 2 and Figure 5 about here
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Of the 6 covariates, only linear age had an impact on activation for reversible compared to non-reversible sentences (at [x = -54, y = -38, z = 20], $Z = 4.2$, 19 voxels at $p < 0.001$) indicating that the effect of reversible vs. non-reversible visual sentences was higher in younger participants, as shown in Figure 6.

There were no other significant effects of reversible relative to non-reversible sentences, even when the analysis was repeated in each age group separately. Therefore, the whole group analysis captured the most prominent source of variance related to reversible versus non-reversible sentences.

==================================
Insert Figure 6 & Tables 3a,b & c about here
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Analysis 2: Reversible and non-reversible sentences in children and adults

Consistent with Analysis 1, a main effect of reversible vs. non-reversible sentences was identified in left T-P at [x=-64, y = -44, z = 24]. The effect was greater for visual than auditory sentences and observed in both age groups (see Figure 7).

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Insert Figure 7 about here
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In summary, we identified one significant effect of reversible versus non-reversible sentences in a left T-P region. The effect was observed in both younger than older participants (see Figure 7) but it was greater in the younger participants (see Figure 6).

Analysis 3: Functional localizers at the group level.

Activations for (i) syntactic and semantic sentence processing, (ii) articulation, and (iii) amodal semantics are shown in Figure 5b. As can be seen, the left T-P region associated above with reversible compared to non-reversible sentences was more activated during the articulation task than any other condition (shown in red). This result indicates that articulatory processes are implicitly engaged during silent sentence processing, most notably for semantically reversible sentences. In contrast,

(i) syntactic and semantic sentence activation (shown in blue) was observed in the left anterior and posterior middle temporal gyrus. These areas were activated by both reversible and non-reversible sentences and there was no effect of sentence type in any of these identified regions. In (ii) other areas associated with articulation were observed in bilateral superior temporal and precentral gyri; and (iii) amodal semantic activation (shown in green) was observed in left lateralized regions in the inferior and middle temporal gyri, pars opercularis and pars orbitalis, and the left putamen (see Table 3c for details).

In short, activation for processing semantically reversible sentences is located in an area that is more strongly associated with articulation rather than syntactic or semantic processing.

Discussion

Semantically reversible sentences are more difficult to process than non-reversible sentence types. As the property of semantic reversibility contributes to the overall difficulty of a sentence across a wide range of grammatical constructions we set out to identify a main effect of semantic reversibility by comparing activation for semantically reversible sentences to that of non-reversible sentences. The results of this whole brain analysis identified a significant effect for reversible relative to non-reversible sentences in a left T-P region.

By including additional linguistic and non-linguistic conditions within our paradigm we were also able to test whether the activation in this left T-P region corresponded to that seen for syntactic/syntactic-semantic processing, sub-articulatory processing, or amodal semantics. This analysis indicated that selective activation for reversible sentences identified in a left T-P region was part of the neuronal system that was more activated by articulation than by any other condition. The pattern of activation in left T-P (as shown in the graph on the bottom panel of Figure 5) indicates that whilst this region was active during sentence processing, it was most active during the repetitive articulation conditions (saying '1','3'). This contrasts with the response of other components of the sentence processing network. For instance, in the left anterior temporal cortex, activation was higher for sentences in comparison to all other conditions (see bottom panel of Figure 5). Likewise, left inferior frontal regions (pars opercularis and pars orbitalis) were strongly activated for sentences but most strongly activated by non-linguistic conditions such as hand action retrieval (see Table 3c and Figure 5).

Previous studies have identified the left temporal-parietal boundary as being actively engaged in both speech perception and speech production tasks (Buchsbaum, Hickok & Humphries, 2001; Hickok, Buchsbaum, Humphries & Muftuler, 2003), and therefore an important site of overlap between the phonological systems for speech input and output (Buchsbaum et al., 2001). For example, Hickok and colleagues report co-ordinates in close proximity to our region for speech and music perception and rehearsal tasks at [x = -51, y = -46, z = 16]. Consistent with these findings, similar co-ordinates are reported by Wise et al. (2001) for a silent word generation task [x = -57, y = -42, z = 22] and by Wildgruber et al. (1999) when participants covertly re-sequenced word-strings [x = -56, y = -40, z = 20]. These studies therefore support the conclusion that this region is activated by tasks which engage verbal working memory. Indeed, the contribution of this region to verbal working memory has been consistently highlighted in the literature (Chein et al, 2003; Hickok et al, 2003; Martin et al, 2003). Hickok et al. suggest that this region supports verbal working memory through its involvement in the maintenance of phonological and acoustic information.

Set in this context our results suggest that the sub-articulatory component of phonological working memory is important in the processing of semantically reversible sentences.

Contrary to some previous studies of sentence complexity (Caplan et al., 1999; 2001; Cooke et al., 2001), the comparison of semantically reversible and non-reversible sentences did not result in increased inferior frontal activation, even when we lowered the statistical threshold to $p<0.05$ uncorrected. Instead, two different inferior frontal regions (pars orbitalis and pars triangularis) were consistently activated by reversible and non-reversible sentences (see Figure 5). The absence of inferior frontal activation in the comparison of reversible versus non-reversible sentences is likely to be explained by our experimental paradigm. Contrary to previous studies of syntactic complexity, we were able to compare reversible and non-reversible sentences while controlling across a range of sentences with different syntactic structures (e.g. active, passive, subject-cleft, object-cleft etc, see Table 1). In addition, we used passive listening and reading tasks that did not require "metalinguistic" analysis (Birdsong, 1989) of either the semantic or syntactic content of the sentences. This would have reduced the demands on executive processing while focusing on the type of processing that occurs during everyday speech perception and reading. The effect of reversible versus non-reversible sentences in passive processing tasks is also consistent with the behavioural literature showing that adults can misinterpret reversible sentences across a range of grammatical constructions (Ferreira, 2003; Herriot, 1969; Kemper & Catlin, 1979; Slobin, 1966; Turner & Rometveit, 1969). Finally, we note that although we did not see increased inferior frontal activation for reversible compared to non-reversible sentences in our passive listening/reading paradigm, this does not exclude the possibility that there would be an effect of reversibility in paradigms that used on-line executive tasks (e.g. semantic or syntactic decisions), or for longer or more complex sentences as used in many of the studies reported by Caplan and colleagues (Caplan et al., 1999; 2001; 2003).

With respect to the role of the inferior frontal activation during both reversible and non-reversible sentences, we found the pattern of response during passive listening and reading was most consistent with amodal semantic processing in accord with many other studies (Noppeney & Price, 2003; 2004; Thompson-Schill et al., 1999; Vandenberghe et al., 1996; Wagner et al., 2001). In particular, we found that inferior frontal activation was not specific to sentence processing (see also Wartenburger et al., 2004), but was most active during a hand-action retrieval task (see Figure 5).

Areas associated with passive syntactic and syntactic-semantic processing were located in the left anterior and posterior temporal cortex, consistent with many previous studies (Awad et al., 2007; Constable et al., 2004; Crinion et al., 2003; 2006; Friederici et al., 2003a; 2003b; Humphries, et al., 2005; 2006; Lindenberg & Scheef, 2007; Scott et al., 2000; Spitsyna et al., 2006; Vandenberghe et al., 2002). This system is likely to include activation related to both syntactic processing and syntactic-semantic integration (hypotheses i and ii respectively). For instance, Humphries et al. (2006) associate anterior temporal regions with the processing of syntactic structure, and Friederici and colleagues (Frederici et al., 2003a; 2003b) have specifically advocated the role of the posterior superior temporal gyrus as being involved in sentence evaluation and syntactic-semantic integration: both these regions are included in our syntax/syntactic-semantic processing network (see Table 3a). Although we cannot conclusively dissociate the functions of these different regions, we can report that there was no evidence for increased activation for reversible relative to non-reversible sentences (at p>0.05 uncorrected within a 6mm diameter) in either the anterior temporal or superior posterior temporal regions. In sum, increased activation for reversible sentences was only detected in a left T-P region that did not correspond to regions engaged in syntactic/syntactic-semantic or amodal semantic processing, but was active for the same subjects during an articulation task.

Our results suggest that semantically reversible sentences increase the demands on a brain region associated with phonological working memory (Wildgruber et al., 1999). However, we still need to consider why the passive processing of semantically reversible sentences should increase the demands on phonological working memory. A potential explanation is that when the use of simple heuristic strategies for sentence processing (such as attending to the semantically relevant content words of a sentence) fail, the representation of a reversible sentence needs to be maintained for longer in phonological working memory in order to allow parts of the sentence to be re-accessed during sentence comprehension

We also observed a stronger effect of reversible relative to non-reversible sentences in our T-P region for children in comparison to adults (see Figure 6). Consistent with this pattern of results, Grossman et al. (2002) found that younger subjects showed more posterior temporal activation [x = -40, y = -36, z = 6] during sentence processing than older subjects, and Wildgruber, et al. (1999) found increased parietal activation [x = -40, y = -44, z = 40] with increasing demands on phonological memory. The effect of age is likely to be a consequence of the proficiency of language use which increases as a product of experience throughout life or the number of years in education. Indeed, Caplan et al. (2003) found increased left temporal-parietal activation [x = -54, y = -32, z = 32] in older subjects as opposed to young adults during a sentence plausibility task but this difference was not apparent when older and younger participants were matched for the number of years in education. In summary, we are proposing that reversible sentences need to be maintained for longer in working memory but this effect is reduced with language proficiency. Thus, as previously suggested by Waters et al. (2003), activation during sentence processing is more likely to vary as a function of processing speed than working memory capacity.

A further observation was that the effect of reversible versus non-reversible sentences was more prominent in the visual modality, which may simply reflect differing task demands in the auditory and visual modalities. For example, sub-articulation is greater for silent reading than listening (Michael et al., 2001). Consistent with this explanation, we found greater left T-P activation at [x = -54, y = -46, z = 24] for the main effect of visual relative to auditory words (Z = 4.2). The types of reversible sentences that we used may also have been more familiar in the visual than auditory domain because some sentence types – namely cleft sentences are not typically experienced in the auditory modality. This may have impeded sentence comprehension in the auditory modality, particularly in children whose experience of language is less extensive than their adult counterparts. Further studies are therefore required for a better understanding of how stimulus modality, age and comprehension ability influence the processing of different types of reversible sentences. Although we predict that the effect of reversible relative to non-reversible sentences is likely to be task dependent, the present study has enabled us to identify reversible sentence processing effects during a passive comprehension task that was not confounded by "meta-linguistic" or executive processes.

Finally, with respect to language disorders that show abnormally high difficulty with reversible sentences there are multiple potential causes. Caplan et al.

(2007) recently suggested that sentence processing difficulties in agrammatic aphasics may be the result of an intermittent reduction in general processing capacity (Caplan et al., 2007). A reduction in processing capacity when processing more complex sentences such as reversible sentences may result in a degraded representation of the linguistic input, which could make the comprehension of complex sentences more challenging when they cannot be solved with simple heuristic strategies. Whilst difficulties in processing semantically reversible sentences may also potentially arise from deficits to syntactic or syntactic-semantic processing, our data are consistent with the perspective that a deficit in phonological working memory may be one cause of apparent problems in syntax comprehension. This account is particularly pertinent in relation to Specific Language Impairment (SLI), since phonological problems have been cited as a potential cause of the disorder in the literature (Gathercole & Baddeley, 1990).

In conclusion, our interpretation is that when processing semantically reversible sentences, sub-articulatory codes must be maintained for a longer period while thematic roles are assigned and the appropriate meaning of the sentence is established.

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Table 1: Details of sentence stimuli composition with examples of sentence types (n = number of items; M = mean; KF = Kucera-Francis)

	Sentence type	n of sentences	Example	Total n of words	Mean number per sentence: syllables	letters	phonemes	M KF frequency	M imageability of content words	M age of acquistion	M concreteness
Reversible sentences	Active	8	"The old dog bites the fox"	6	7	25	17	122	558	208	539
	Passive	8	"The rat is sniffed by the grey squirrel"	8	10	32	25	57	565	242	553
	Subject-cleft	8	"It is the dancer that hugs the clown"	8	9	30	22	108	572	293	562
	Object-cleft	8	"It is the cook that loves the woman"	8	9	29	22	179	565	228	544
	Locative	4	"The circle is in the gold star"	7	8	25	19	88	573	245	580
	Dative	4	"Give the happy boy to the girl"	7	8	24	19	139	534	204	509
	Total	40	*Mean*	*7*	*8*	*27*	*21*	*115*	*561*	*237*	*548*
Non-reversible sentences	Active	8	"The rich queen spends the money"	6	8	26	20	115	525	306	515
	Passive	8	"The giant safe is locked by the guard"	8	10	31	24	74	505	357	494
	Subject-cleft	8	"It is the drunk that starts the fight"	8	9	30	24	182	506	306	470
	Object-cleft	8	"It is the dress that the model hates"	8	10	31	25	87	503	315	473
	Locative	4	"The marble temple is in the field"	7	9	26	21	210	554	324	548
	Dative	4	"Put the salt on the plain meal"	7	9	28	23	172	483	310	471
	Total	40	*Mean*	*7*	*9*	*28*	*23*	*140*	*513*	*320*	*495*

* Non-reversible sentences were in the main strongly non-reversible, where the constraints set for the sentence stimuli permitted.

Table 2: Regions that showed increased activation for reversible relative to non-reversible sentences.

REVERSIBLES >NON-REVERSIBLES: Left temporal-parietal boundary

	Main effect					Visual sentences					Auditory sentences				
Analysis	*x*	*y*	*z*	*Z* score	*n* voxels	*x*	*y*	*z*	*Z* score	*n* voxels	*x*	*y*	*z*	*Z* score	*n* voxels
All participants	**-58**	**-42**	**22**	3.5	22	**-58**	**-44**	**20**	4.0	89	-58	-40	24	2.3	62
	-62	-48	22	3.3		-52	-44	26	3.9		**-64**	**-40**	**28**	2.8	
Children only	**-58**	**-44**	**20**	2.7		**-52**	**-34**	**20**	4.2		**-64**	**-38**	**28**	2.4	
Adults only	**-64**	**-46**	**24**	2.4		**-62**	**-48**	**20**	2.3		**-62**	**-42**	**26**	2.4	

Co-ordinates [x, y, z] are reported in MNI space. Activation for visual sentences across all participants was significant at $p<0.05$ corrected for extent across the whole brain. *n* voxels = the number of voxels significant at $p<0.001$ uncorrected for visual sentences and $p<0.05$ uncorrected for auditory sentences. Peak voxels are shown in bold text. Those from all participants come from Analysis 1, those for Children and Adults alone come from Analysis 2.

Table 3a

(a)

Syntax / Syntactic-semantic processing						
				Sentences		**Sentence > All**
Anatomical location	*x*	*y*	*z*	*n* voxels	*Z* score	*Z* score
Anterior temporal gyrus	-56	0	-16	**10**	Inf.	6.7
	-58	-18	-6	**49**	Inf.	6.9
Posterior temporal gyrus	-48	-42	0	**10**	Inf.	Inf.
	-64	-50	10	**14**	Inf.	Inf.
	-48	-60	20	**27**	5.2	6.2
	-60	-62	16	**5**	4.9	5.0

n voxels = the number of voxels significant at p<0.001 uncorrected.

Table 3b

(b)

Articulation:							
					Articulation		**Articulation > All**
Hemisphere	Anatomical location	*x*	*y*	*z*	*n* voxels	*Z* score	*Z* score
Left	Temporal-parietal boundary	-50	-46	20	**40**	4.9	3.7
		-62	-40	14		5.0	4.1
Left	Pre/post-central gyrus	-46	-14	36	**550**	Inf.	Inf.
		-50	-12	32		Inf.	Inf.
		-60	-4	18		Inf.	Inf.
Right	Temporal-parietal boundary	62	-40	14	**71**	5.8	5.5
		58	-34	18		5.3	5.3
Right	Pre/post-central gyrus	50	-12	44	**586**	Inf.	Inf.
		48	-10	34		Inf.	Inf.
		52	-6	28		Inf.	Inf.
		58	-4	24		Inf.	Inf.

n voxels = the number of voxels significant at p<0.001 uncorrected. Co-ordinates highlighted by a box are those closest to the peak activation for reversible sentences.

Table 3c:

(c)

Amodal semantics:					
	Left hemisphere				
Anatomical location	*x*	*y*	*z*	*Z* score	*n* voxels
Middle temporal gyrus	-58	-58	2	Inf.	**125**
	-54	-64	10	5.0	
Inferior frontal operculis	-50	10	22	6.5	**90**
	-48	16	28	4.8	
orbitalis	-36	26	-2	4.9	**58**
	-50	18	-8	4.0	
Putamen	-24	-4	12	6.4	**43**
	-22	0	12	6.3	
	-22	-6	16	6.0	

n voxels = the number of voxels significant at $p<0.001$ uncorrected.

Figure captions:

Figure 1: Examples of semantically reversible and non-reversible sentences. The subject and object of a reversible sentence may be reversed and still produce a meaningful sentence, whereas non-reversible sentences become semantically anomalous when they are reversed. In thematic role assignment the *agent* is the entity acting on the object or person in the sentence, whilst the entity or person being acted upon is referred to as the *patient.*

Figure 2: Examples of stimuli presented in the object conditions. In the activation task (objects with hand actions), participants were instructed to use their right hand to make an action as if using the object. In each of the three baseline tasks (objects, animals and non-objects) participants made a rocking motion (also with their right hand) when viewing the stimulus.

Figure 3: Experimental design. All condition blocks for a single session are depicted here. One run through each type of task (A, V, M, and O) totalled 8 blocks. The order of each type of task was counterbalanced within session for each run (3 runs x 8 blocks each = 24 blocks). Session order was counterbalanced across participants (x 4 sessions), as were sentence stimuli (x 2 sets), giving a total of 8 (2 x 4) condition orders.

Figure 4: Procedure. Timing and presentation of tasks, from left to right: (1) auditory sentence processing, (2) visual sentence processing, (3) object action retrieval, and (4) articulation.

Figure 5: Activation for (a) reversible vs. non-reversible sentences (b) syntactic and semantic sentence processing in blue, amodal semantics in green and articulation in red. The statistical threshold for both (a) and (b) was $p<0.001$ uncorrected for height but $p<0.05$ corrected for extent. Plots show the parameter estimates for each condition in each of the labelled regions. The red bars are the 90% confidence intervals. On the x-axis the conditions correspond to contrasts 7-13 that were entered into group level analysis 3 (see Methods section for details): auditory sentences (AS), visual sentences (VS), auditory words (AW), visual words (VW), object action retrieval (O), articulation (A), and mouth movements (M). The y-axis shows effect sizes as the mean of the beta value from the first level analysis (i.e. the percentage increase in activation relative to the global mean). These plots show that inferior frontal regions responded to both non-linguistic and linguistic stimuli. Activation of the posterior superior temporal gyrus is greatest in sentence contrasts (AS & VS). Activation on the left temporal-parietal boundary is greatest in the articulation contrast (A). The peak for semantically reversible sentence falls within this region.

Figure 6: scatter plot showing the relationship between age and activation at the peak voxel [x = -54, y = -38, z = 20] for the significant effect of age on visual reversible over and above non-reversible sentences ($Z = 4.2$, 19 voxels at $p < 0.001$). The values on the y-axis represent effect size derived from β values for each participant.

Figure 7: shows a plot of the parameter estimates according to age group, processing modality and sentence type, at the peak co-ordinate of the main effect for reversible vs. non reversible sentences in this analysis [x = -64, y = -44, z = 24]. The red bars are the 90% confidence intervals. On the x-axis the conditions correspond to contrasts 1-4 from each age group as entered into group level analysis 2 (see Methods section for details): (1) auditory reversible sentences, (2) auditory non-reversible sentences, (3) visual reversible sentences, and (4) visual non-reversible sentences. The y-axis shows effect sizes as the mean of the beta value from the first level analysis (i.e. the percentage increase in activation relative to the global mean). This plot shows that both age-groups show a similar activation profile across sentence types.

Reversible sentence:

“The leopard races the young lion”

[subject] – [verb] … [object]

Reversed: *“The lion races the young leopard”*

Non-reversible sentence:

“The dog chews the bone”

Reversed: *“The bone chews the dog”*

Figure 1: Examples of semantically reversible and non-reversible sentences. The subject and object of a reversible sentence may be reversed and still produce a meaningful sentence, whereas non-reversible sentences become semantically anomalous when they are reversed. In thematic role assignment the agent is the entity acting on the object or person in the sentence, whilst the entity or person being acted upon is referred to as the patient.
28x24mm (500 x 500 DPI)

Figure 2: Examples of stimuli presented in the object conditions. In the activation task (objects with hand actions), participants were instructed to use their right hand to make an action as if using the object. In each of the three baseline tasks (objects, animals and non-objects) participants made a rocking motion (also with their right hand) when viewing the stimulus.
28x34mm (500 x 500 DPI)

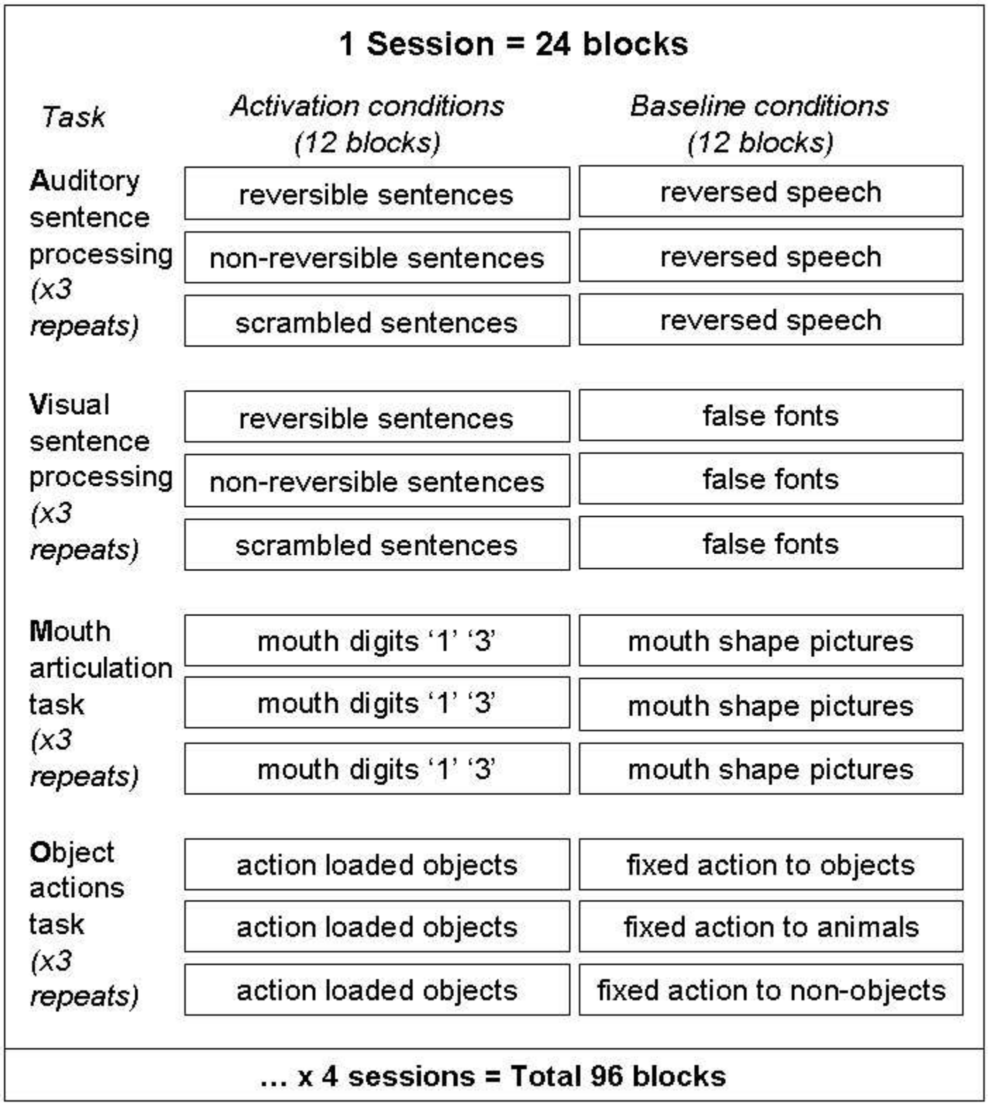


Figure 3: Experimental design. All condition blocks for a single session are depicted here. One run through each type of task (A, V, M, and O) totalled 8 blocks. The order of each type of task was counterbalanced within session for each run (3 runs x 8 blocks each = 24 blocks). Session order was counterbalanced across participants (x 4 sessions), as were sentence stimuli (x 2 sets), giving a total of 8 (2 x 4) condition orders.
36x40mm (500 x 500 DPI)

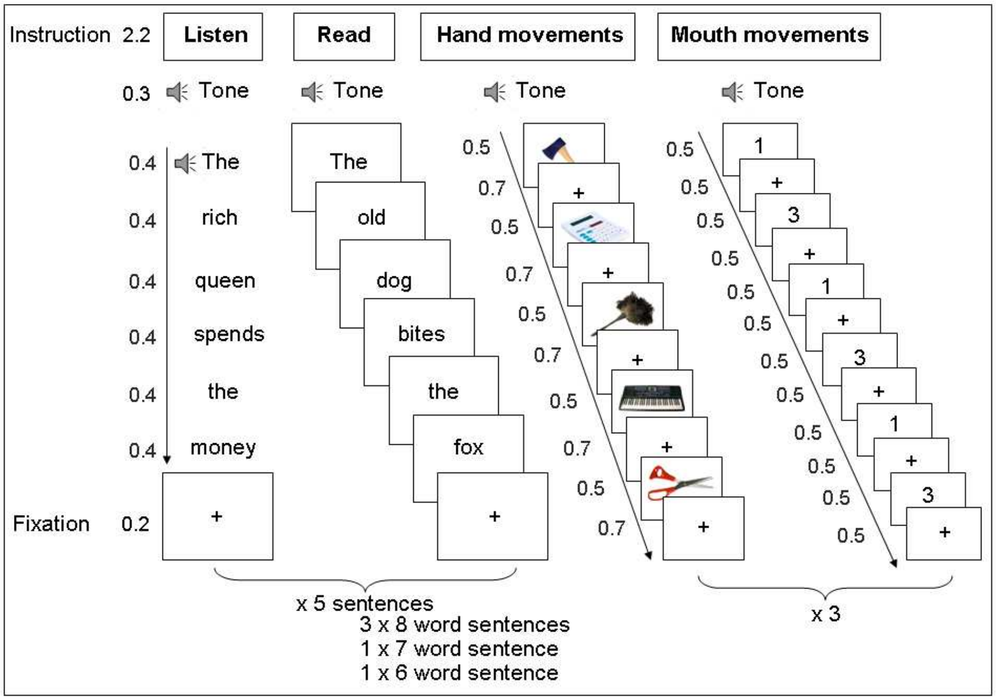


Figure 4: Procedure. Timing and presentation of tasks, from left to right: (1) auditory sentence processing, (2) visual sentence processing, (3) object action retrieval, and (4) articulation.
48x33mm (500 x 500 DPI)

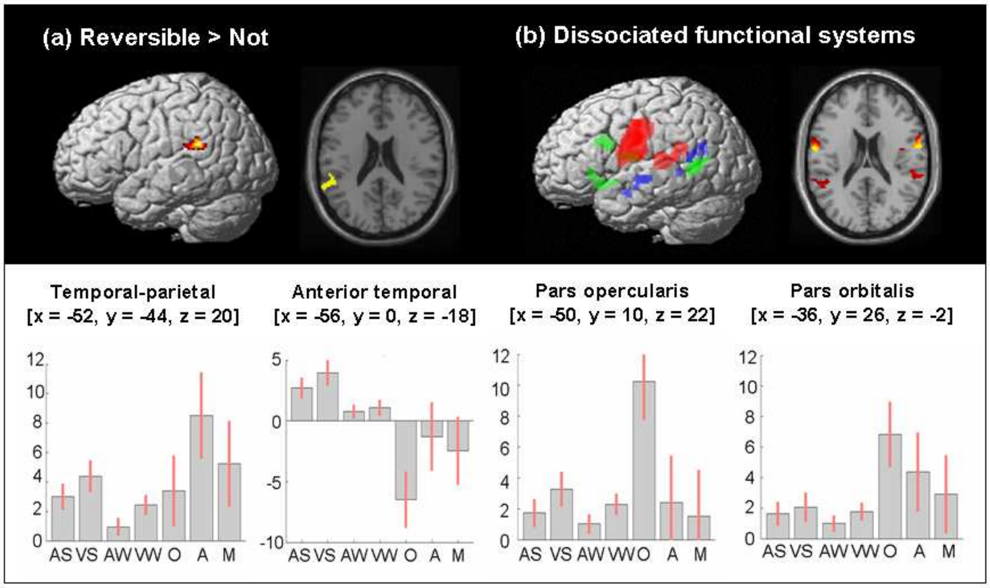
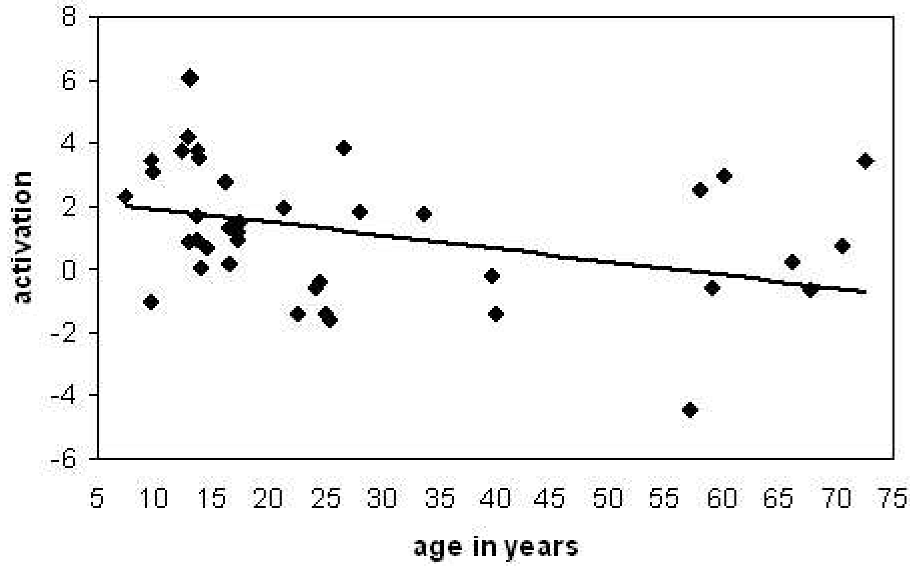


Figure 5: Activation for (a) reversible vs. non-reversible sentences (b) syntactic and semantic sentence processing in blue, amodal semantics in green and articulation in red. The statistical threshold for both (a) and (b) was $p<0.001$ uncorrected for height but $p<0.05$ corrected for extent. Plots show the parameter estimates for each condition in each of the labelled regions. The red bars are the 90% confidence intervals. On the x-axis the conditions correspond to contrasts 7-13 that were entered into group level analysis 3 (see Methods section for details): auditory sentences (AS), visual sentences (VS), auditory words (AW), visual words (VW), object action retrieval (O), articulation (A), and mouth movements (M). The y-axis shows effect sizes as the mean of the beta value from the first level analysis (i.e. the percentage increase in activation relative to the global mean). These plots show that inferior frontal regions responded to both non-linguistic and linguistic stimuli. Activation of the posterior superior temporal gyrus is greatest in sentence contrasts (AS & VS). Activation on the left temporal-parietal boundary is greatest in the articulation contrast (A). The peak for semantically reversible sentence falls within this region.
44x26mm (500 x 500 DPI)



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23x15mm (500 x 500 DPI)

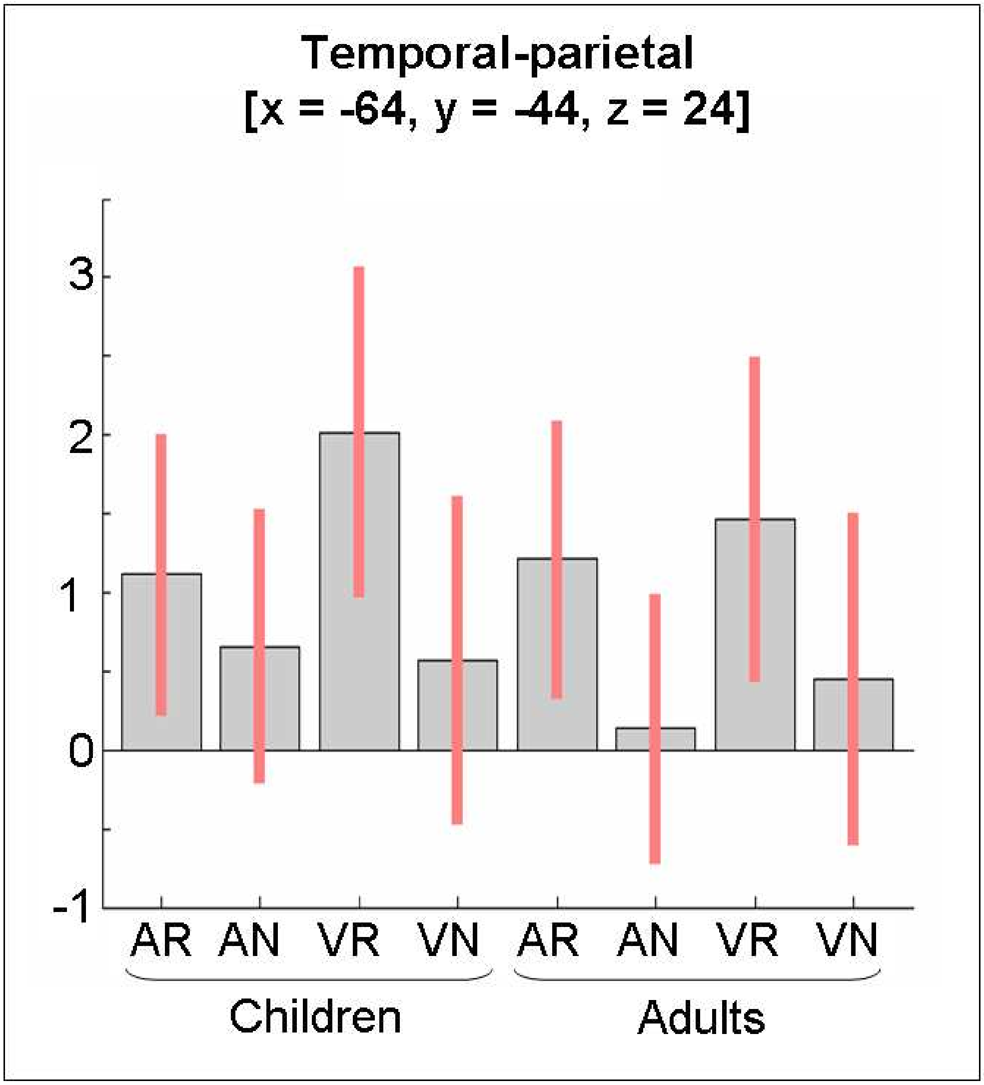

Figure 7: shows a plot of the parameter estimates according to age group, processing modality and sentence type, at the peak co-ordinate of the main effect for reversible vs. non reversible sentences in this analysis [x = -64, y = -44, z = 24]. The red bars are the 90% confidence intervals. On the x-axis the conditions correspond to contrasts 1-4 from each age group as entered into group level analysis 2 (see Methods section for details): (1) auditory reversible sentences, (2) auditory non-reversible sentences, (3) visual reversible sentences, and (4) visual non-reversible sentences. The y-axis shows effect sizes as the mean of the beta value from the first level analysis (i.e. the percentage increase in activation relative to the global mean). This plot shows that both age-groups show a similar activation profile across sentence types.
34x38mm (500 x 500 DPI)