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Research Report
Lexical ambiguity in sentence comprehension
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ABSTRACT

An event-related fMRI paradigm was used to investigate brain activity during the reading of sentences containing either a lexically ambiguous word or an unambiguous control word. Higher levels of activation occurred during the reading of sentences containing a lexical ambiguity. Furthermore, the activated cortical network differed, depending on: (1) whether the sentence contained a *balanced* (i.e., both meanings equally likely) or a *biased* (i.e., one meaning more likely than other meanings) ambiguous word; and, (2) the working memory capacity of the individual as assessed by reading span. The findings suggest that encountering a lexical ambiguity is dealt with by activating multiple meanings utilizing processes involving both hemispheres. When an early interpretation of a biased ambiguous word is later disambiguated to the subordinate meaning, the superior frontal cortex activates in response to the coherence break and the right inferior frontal gyrus and the insula activate, possibly to suppress the incorrect interpretation. Negative correlations between reading span scores and activation in the right hemisphere for both types of ambiguous words suggest that readers with lower spans are more likely to involve show right hemisphere involvement in the processing of the ambiguity. A positive correlation between reading span scores and insula activation appearing only for biased sentences disambiguated to the subordinate meaning indicates that individuals with higher spans were more likely to initially maintain both meanings and as a result had to suppress the unintended dominant meaning.

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1. Introduction

One of the building blocks of language comprehension is the ability to access the meaning of words as they are encountered and to develop an interpretation that is consistent with the context. This process becomes particularly interesting at a choice point in understanding, as is the case with lexically ambiguous words. When a word has multiple meanings, one meaning must be selected while somehow retaining the possibility of using the alternative meaning. Additionally, the working memory capacity of individual readers affects their

ability to maintain various representations in the process of understanding a sentence (Miyake et al., 1994). Further complicating this phenomenon, ambiguous words vary in the *strength* or *frequency* of their alternative meanings (e.g., Swinney, 1979; Rayner and Duffy, 1986; MacDonald et al., 1994) leading to situations in which the likelihood of maintaining multiple meanings could be dependent on their relative frequencies. In some cases, the ultimately incorrect interpretation may initially be selected, leading to a semantically incoherent sentence representation and hence to a re-analysis of the meaning and a suppression of the misfitting interpreta-

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tion. By examining how the cortical networks change in the processing of different types of ambiguity, it should be possible to fractionate some of the component processes of ambiguity resolution and relate them to individual differences in working memory capacity.

1.1. Behavioral research and implications

Behavioral research has shown that there is a cost to ambiguity in that it takes longer to read a sentence that contains ambiguous words (e.g., Duffy et al., 1988; Miyake et al., 1994; Rayner and Duffy, 1986). Rayner and Duffy (1986) presented participants with sentences that contained ambiguous words that were either biased or balanced. A biased ambiguous word is one whose two meanings are asymmetric in frequency, such that one meaning is dominant and the other subordinate, as is the case with the word *ball* in the following sentence:

Biased, disambiguated to subordinate meaning

This time the *ball* was moved because it was always so well attended.

A balanced ambiguous word is one with two equally likely meanings. The word *pitcher* in the following sentence is an example of such a word:

Balanced

Of course the *pitcher* was often forgotten because it was kept on the back of a high shelf.

They found that readers' eyes remained longer on a balanced ambiguous word than a matched control word but that there was no such ambiguity effect for biased ambiguous words. Interestingly, both types of ambiguous words were accompanied by an increase in reading times on the post-target region with an additional cost for the biased ambiguous words. They suggested that one of the two main meanings was selected during the initial encounter with the word, occasionally leading to the wrong interpretation for the balanced ambiguous words but always leading to the wrong interpretation for the biased ambiguous words. Duffy et al. (1988) followed up this experiment by showing that prior biasing context could affect the order in which words were selected but suggested that multiple meanings are exhaustively accessed.

Research on lexical ambiguity has been guided largely by theories based on behavioral studies using methods including: reading times, eye movements, cross modal priming, probe response times and electrophysiological recording. Although advances have been made in understanding the neural basis of lexical ambiguity processing, many of these advances have come from neuropsychological patient data and ERP or MEG data. Surprisingly little research on lexical ambiguity has been done utilizing brain imaging techniques such as fMRI. What little we know of the brain activity during the processing of lexical ambiguities in context comes from only a tiny number of studies (e.g. Rodd et al., 2005).

1.2. Semantic knowledge

There have been some relevant imaging findings concerning meaning retrieval and selection for ambiguous words presented without a context (for a review see Bookheimer, 2002). Results from a range of studies indicate that processing of meaning retrieval, selection and maintenance involves the left inferior frontal gyrus, left superior temporal gyrus and possibly their right hemisphere homologues. The majority of early semantic investigations examined meaning retrieval, search and selection primarily out of context or when the task involved some type of semantic judgment other than simply reading (e.g., Fiez, 1997; Gabrieli et al., 1998; Gold and Buckner, 2002; Petersen et al., 1989; Wagner et al., 1997). Many of these semantic processing studies have implicated the left inferior frontal gyrus as active whenever an individual has to perform some type of semantic analysis. Several researchers (e.g., Thompson-Schill et al., 1999) have suggested that the role of the inferior frontal gyrus is for a more general process of selection among alternatives rather than semantic processing. The second most often cited region for semantic processing is the left temporal lobe. The primary source for this localization comes from categorical processing tasks (see Caramazza et al., 1990 and Price, 2000 for a review). In addition to finding that the left middle and superior temporal lobes activate for categorical decisions (such as living versus non-living judgments), studies have also found the fusiform gyrus (previously associated with object processing) to activate (e.g., Ishai et al., 1999). Still other researchers have suggested that semantic meaning is diffusely represented across the cortex, perhaps on the basis of featural properties (Martin and Chao, 2001; Goldberg et al., in press). Chan et al. (2004) proposed that a semantic ambiguity processing network consisted of left frontal regions, the anterior cingulate and the right inferior parietal lobe. They found that these regions were more active when viewing semantically ambiguous Chinese characters than when viewing semantically precise Chinese characters.

Examining semantic processing in sentential contexts rather than on a single-word basis enables a network level description of the various areas that support semantic processing. This approach was taken by Rodd et al. (2005) who examined the activation associated with listening to speech containing either highly ambiguous sentences or matched low-ambiguity sentences. The highly ambiguous sentences resulted in increased activation in the left inferior temporal cortex and the left and right inferior frontal cortex.

It is noteworthy that both Chan et al. and Rudd et al. also found some right hemisphere activation (right inferior parietal for Chan et al. and right inferior frontal for Rudd et al.) even though both studies examined language tasks. This is consistent with evidence that patients with right-hemisphere damage have difficulty connecting and integrating semantically distant concepts (Brownell and Martino, 1998; Beeman, 1993; Bihle et al., 1986; Weylman et al., 1989; Brownell et al., 1983). According to Beeman's coarse coding hypothesis, the left hemisphere uses fine semantic coding to quickly select a small number of relevant meanings, while the right hemisphere uses a coarse semantic coding scheme in which it weakly activates a broad spectrum of meanings and features (Beeman, 1993; 1998); the less rapid activation of these right

hemisphere coarse semantic fields presumably allows more than one sense of a word's meanings to be accessed (Beeman et al., 1994; Chiarello et al., 1990; Nakagawa, 1991). ERP data have supported the hypothesis of greater duration of activation of semantic fields in the right hemisphere (Burgess and Simpson, 1988; Swaab et al., 1998). It is therefore possible that the imaging of individuals reading ambiguous words within a sentence context could provide evidence for the role of the right hemisphere when words have multiple meanings in addition to the activation of left inferior frontal gyrus and left superior temporal gyrus associated with conventional sentence comprehension.

1.3. Working memory capacity

Miyake et al. (1994) suggested that an individual's working memory capacity is an additional factor that may influence the manner in which lexical ambiguities within sentences are processed. They found a pattern of reading times across the range of words in the post-target region (the words following the ambiguous word) that suggested a reader's working memory capacity influenced the length of time alternate interpretations were maintained; that is, the high span participants maintained alternate meanings even for the subordinate meaning of biased ambiguous words longer than did mid or low spans. It is likely that either the conditions under which additional cortical networks are recruited to process ambiguities or the degree to which additional networks are recruited are influenced by the reader's working memory capacity during reading.

Few neuroimaging studies have investigated activation differences as a function of working memory capacity. Osaka et al. (2003) found that high span participants had more activation than low span participants in the anterior cingulate cortex region during a listening span task. Reichle et al. (2000) found higher levels of activation in a sentence–picture verification task for verbal low span participants in Broca area when using a verbal strategy. They also found higher levels of activation for participants with poorer spatial skills when using a visual strategy. These results suggest that participants with lower skills show more activation. In the case of lexical ambiguity, this processing load most likely occurs either in areas specialized for maintaining semantic interpretations of a sentence, such as the inferior frontal gyrus, or perhaps for maintaining the availability of the alternate meaning, such as the right hemisphere (Beeman, 1998).

1.4. Summary and fMRI implications

In the study reported below, event-related functional imaging was used to investigate cortical activity during the reading of sentences containing either lexically ambiguous words or matched control words. The ambiguous words were of two classes: biased and balanced. These two types of ambiguous words allow investigation of how the cortical networks of the brain function when the ambiguity leads to *early* (biased) or *late* (balanced) selection of meaning. For the majority of the balanced ambiguous words, one would expect that when the ambiguous word is first encountered, multiple meanings are accessed maintained to some degree during the reading of the

remainder of the sentence. In contrast, the biased words should result in selection of the dominant meaning, leading to a *garden path* effect in which the wrong interpretation has been pursued. Selecting an initial interpretation of an ambiguous word that later turns out to be incorrect creates a semantic incoherence. Several researchers have shown that prefrontal regions become active in response to the incoherence (Ferstl and von Cramon, 2001, 2002). Thus, it is likely that additional activation appears in a region serving as a coherence monitor (Mason and Just, *in press*). This coherence monitor could be an indication that the incoherence has to be resolved.

To resolve the incoherence, the alternative meaning of the ambiguous word likely has to be retrieved and a semantic reanalysis has to be performed. Most likely this involves the same left inferior frontal gyrus activation that was involved in the original analysis. The right hemisphere homologue could exhibit additional activation as a result of the increase in the cognitive workload involved (Just et al., 1996; Keller et al., 2001). Additionally, if the less likely alternative meaning must be retrieved, this could account for the greater duration of activation of the semantic fields in the right hemisphere (Burgess and Simpson, 1988; Swaab et al., 1998). During this act of re-interpreting the sentence, the initial (i.e., the incorrect) interpretation remains available and may need to be suppressed.

Gernsbacher and colleagues have suggested that the act of suppression of an inappropriate meaning involves a general cognitive suppression mechanism (Gernsbacher, 1990, 1991; Faust and Gernsbacher, 1996; Gernsbacher and St. John, 2001). How this suppression might be manifested in brain activation is less clear. Hemispheric presentation of words has indicated that both the left and right hemispheres have occasionally shown evidence of suppression (e.g., Faust and Gernsbacher, 1996) but very little localization is possible from these studies. Additionally, neuropsychological research has shown that right-hemisphere-damaged patients have difficulty suppressing inappropriate meanings (Tompkins et al., 2000; Klepousniotou and Baum, 2005). This suggests that the right hemisphere may play a role in suppression, however localization within the right hemisphere is limited. Perhaps better localization of the cortical basis of suppression may come from fMRI attention tasks (for a review see: Posner, 2004). In some cases, the anterior cingulate and the insula have been shown to activate during experiments in which the participant had to engage in thought suppression or shifting of attention (e.g., Wyland et al., 2003). Finally, one might expect differential engagement of these networks as a function of the reader's working memory capacity.

2. Results

2.1. Distribution of activation

Overall, reading a sentence containing an ambiguous word activated the left inferior frontal gyrus more than did reading a sentence containing a matched control word. Additional small clusters of activation were localized between the superior and middle frontal gyri in both hemispheres, although the activa-

tion was larger in the superior frontal gyrus on the left and the middle frontal gyrus on the right. This effect not only arose from the sentences in which the wrong interpretation (i.e., the biased, subordinate sentences) had been selected but also from balanced ambiguities. The sentences containing balanced ambiguous words activated only the left inferior frontal gyrus when contrasted with sentences containing unambiguous matched control words. The biased condition produced additional activation that the balanced ambiguities did not. First, there was extra activation in the left inferior frontal gyrus; the extent of this activation was above and beyond the extra activation evoked by balanced ambiguities. Second, the right inferior frontal gyrus also showed an increase in activation for biased ambiguous words. This bilateral extra activation in the inferior frontal region may be due to semantic reanalysis required by these sentences. Biased ambiguities also produced bilateral superior frontal activation. The surface rendering of the ambiguity effect as well as those of the biased and balanced ambiguity effects can be seen in Fig. 1. The extent of the activation is reported in Table 1.

A direct contrast between the Biased Ambiguous sentences minus the Balanced Ambiguous sentences indicated activation bilaterally in the insula as well as a small cluster in the inferior portion of the inferior frontal gyrus. The surface rendering of the direct comparison between the activation associated with reading the biased and the balanced ambiguous sentences is shown in Fig. 2. The extent of the activation is listed in Table 1.

2.2. Distribution of activation as correlated with an individual's reading span

According to Miyake et al. (1994), lexically ambiguous sentences are processed differently depending on individual working memory constraints. In order to investigate how an individual's working memory affected the cortical network underlying the processing of lexical ambiguities, the activation was correlated with reading span. In general, readers with lower reading spans relied more heavily on the right hemisphere to process ambiguities. In particular, the right inferior frontal and the right superior temporal areas were negatively correlated with RSPAN. For the Balanced Ambiguous sentences, low spans utilized the right inferior frontal gyrus and the right middle temporal gyrus more than high spans as indicated by the negative correlation with RSPAN. For the Biased Ambiguous sentences, activation negatively correlated with RSPAN was found in the left superior frontal gyrus and an area within the right superior temporal lobe. No areas of activation were positively correlated with RSPAN in the ambiguity effect contrasts; however, that was not true in the direct comparisons of the two types of ambiguous sentences. For the contrast of Balanced Ambiguous sentences minus Biased Ambiguous sentences, activation was again negatively correlated with RSPAN in several areas. In this instance, the left and right superior temporal regions were utilized more by the low spans in the balanced than the biased ambiguous sentences. For the opposite contrast, only the medial frontal region showed a negative correlation with RSPAN. Also in the Biased Ambiguous sentences minus the Balanced Ambiguous sentences, the only case in which activation was positively

correlated with RSPAN appeared. This suggests that the higher an individual's reading span, the greater the activity in the right and left insula regions for Biased over Balanced Ambiguous sentences. For simplicity, the negative correlation of the overall Ambiguity effect and the RSPAN correlations with the direct contrasts are shown in Fig. 3. All regions correlated with RSPAN for the complete set of contrasts can be seen in Table 2.

3. Discussion

Overall, the distribution of activation supports several conclusions about the manner in which semantic ambiguities are processed in context. First, there was additional left inferior frontal gyrus activation for any ambiguity, indicating that the lexical ambiguity evokes extra processing that could be attributable to generation, maintenance, and selection of multiple meanings. Second, the additional activation in right inferior frontal gyrus for the biased ambiguous words when compared to unambiguous sentences suggests either (A) spillover of processing due to the difficulty that arose in selection of the incorrect meaning or (B) a right hemisphere-based search of coarse semantic representation; these coarse semantic fields may be present to help resolve secondary meanings associated with biased ambiguous words. Third, the bilateral middle and superior frontal activation for the sentences containing biased ambiguous words may be indicative of a coherence monitoring process. This monitor activates in response to the mismatch between an incorrect initial interpretation (the dominant meaning) and the disambiguating information in the text (supporting the subordinate meaning). The right inferior frontal and insula region also activated for the biased meanings, consistent with the possibility that it was necessary to suppress the incorrect dominant interpretation in those cases.

3.1. The base network: Generation, maintenance, and selection of multiple meanings

The left inferior frontal gyrus was engaged whenever a meaning was selected in the presence of an ambiguity and an interpretation for that meaning had been generated. This activation could be a result of additional activation due to the access of multiple meanings or could be due to some subset of the sentences being processed incorrectly and needing to be re-parsed. The current data set cannot distinguish between these two hypotheses.

3.2. The base network: Reanalysis after selection of the incorrect meaning

For the biased ambiguities that were disambiguated to the less likely meaning, most likely the incorrect meaning was selected. This could be similar to a syntactic *garden path* effect, in which the sentence must be reinterpreted with the correct meaning and the incorrect meaning is discarded. A comparison of the activation maps for the two types of ambiguous sentences suggests that the biased condition (which evokes this type of *garden path*) produced additional activation bilaterally in the inferior frontal region compared to the balanced

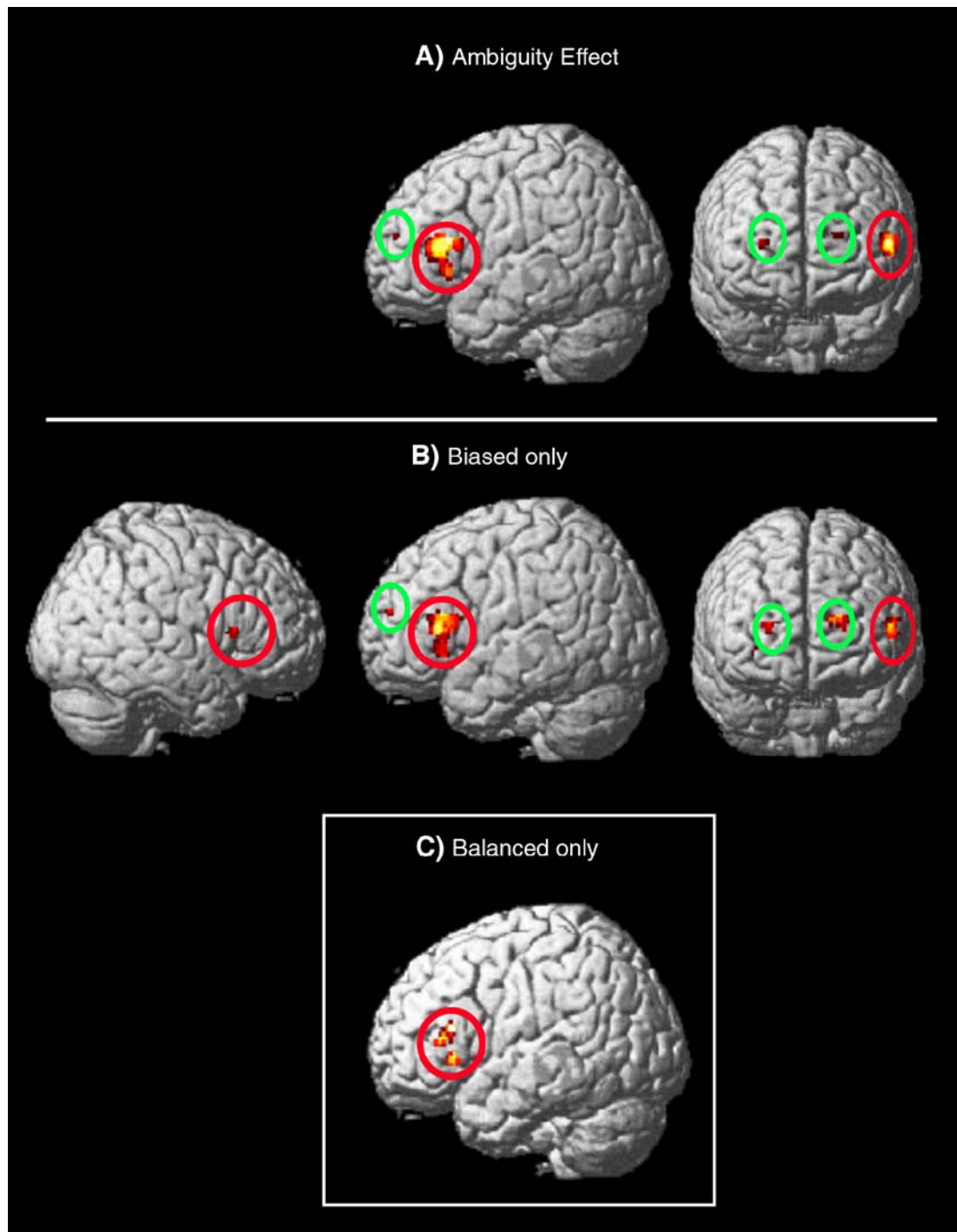


Fig. 1 – (A) The left inferior frontal (red circles) and superior frontal (green circles) regions that increase in activation for the contrast of sentences containing ambiguous words minus sentences containing matched unambiguous words. Activation is projected onto the surface rendering. (B) The ambiguity effect for sentences containing the biased ambiguous words. Note that the right inferior frontal region is also activated (red circle). (C) The ambiguity effect for sentences containing the balanced ambiguous words, only the left inferior frontal region is active. The corresponding cortical regions, cluster sizes, peak *T*-values and MNI coordinates can be found in [Table 1](#).

ambiguities. This bilateral extra activation in the inferior frontal region may be due to semantic reanalysis required by these sentences. Biased ambiguities also produced bilateral superior frontal activation. This activation may be attributed

to coherence monitoring. Other studies have also found evidence of this in the superior frontal/dorsal lateral pre-frontal cortex region (Ferstl and von Cramon, 2001; Mason and Just, *in press*).

Table 1 – Areas of activation for the ambiguity effect

Cortical region	Cluster size	Peak T-value	MNI coordinates		
			x	y	z
<i>(A) Ambiguous versus Unambiguous</i>					
Left inferior frontal	422	5.79	-28	12	16
Right caudate/putamen	84	5.78	24	16	12
Right middle and superior frontal	20	4.43	26	46	16
Left caudate	12	4.22	-8	18	6
Right caudate	17	4.07	12	18	8
Left superior and middle frontal	9	3.65	-20	54	18
<i>(B) Biased Ambiguous</i>					
Right inferior frontal/insula	168	8.60	34	30	6
Right superior and middle frontal	80	7.27	24	46	16
Left superior and middle frontal	117	6.17	-16	46	14
Left inferior frontal/insula	319	5.99	-52	26	12
Right putamen/caudate	139	5.95	24	12	10
Left caudate	37	5.52	-12	20	12
Left insula	35	4.50	-24	22	2
Left thalamus/hippocampus	45	4.35	-22	-28	0
Right orbital frontal	16	3.71	46	18	10
Left thalamus	8	3.70	-12	-12	10
<i>(C) Balanced Ambiguous</i>					
Left inferior frontal	23	4.71	-42	32	10
Left inferior frontal	34	4.70	-46	24	2
Left caudate	39	4.27	-8	4	8
Left inferior frontal	38	3.63	-56	26	16
Left caudate/putamen	7	3.56	-16	8	14
<i>(D) Biased minus Balanced</i>					
Right insula	50	6.14	42	12	-8
Left insula	20	4.58	-40	14	-6
Left inferior frontal	9	3.81	-42	26	-2
The threshold for significant activation was $p < 0.005$ for a spatial extent of at least 6 voxels, uncorrected for multiple comparisons. Region labels apply to the entire extent of the cluster. T-values and MNI coordinates are for the peak-activated voxel in each cluster only.					

3.3. The base network: Suppression of incorrect meanings

The insula and a small cluster in the inferior portion of the inferior frontal gyrus were the only areas of activation in a direct contrast of the two types of ambiguous sentences (Biased – Balanced). The extra activation in the inferior portion of the inferior frontal gyrus suggests that a syntactic reanalysis is made of the biased sentences that are disambiguated to the subordinate meaning. This reanalysis hypothesis is supported by the finding of activation in the insula. The insula has been shown to activate during experiments in which the participant had to engage in thought suppression or shifting of attention (Wyland et al., 2003). Although it does not appear in a contrast of the two types of ambiguous words, the caudate is consistently active during the reading of ambiguous sentences. This region includes the basal ganglia, which are consistently found in action selection (Bergman et al., 1998);

moreover, it has been found to be active during the processing of syntactically ambiguous sentences (Stowe et al., 2004). The fact that it appears in both types of ambiguous sentences indicates that if it does play an inhibitory role, this role must be more general. In the case of balanced ambiguous words, it may help to inhibit the unselected meaning whereas for biased ambiguous words it may help to inhibit an incorrectly selected meaning.

3.4. Capacity influences on the cortical network for processing ambiguities

The influence of reading span on brain activation suggests a new perspective on the cortical network that processes lexical ambiguity. The results suggest that as long as memory resources are adequate, multiple meanings of the ambiguous word may be maintained for awhile. The overall activation of right inferior frontal and right superior temporal activation for ambiguous sentences indicates that these regions were recruited to handle multiple meanings. The negative correlation of this activation with reading span suggests that it was more difficult for low spans to access and maintain the multiple meanings than for the high spans. Furthermore, this was more evident in balanced ambiguous sentences than in biased ambiguous sentences.

One speculative account is that with balanced ambiguous words, both meanings become available at the same time (Swinney 1979; Rayner and Duffy, 1986) such that low spans as well as high spans have little choice but to access and try to maintain both representations. The coarse coding of the word meanings by the right hemisphere (Beeman, 1998) may help to maintain the lower frequency interpretation (MacDonald et al., 1994). It is possible that the high spans are able to access and maintain and actively process both meanings in the left hemisphere (or minimally use the right hemisphere before meaning is transferred to the left) but the low spans have to recruit the right hemisphere for maintenance and have little ability to process both meanings. In contrast, while both low and high spans may have some initial right hemisphere activation associated with the ambiguity, the high spans maintain the availability of the subordinate meaning while selecting the dominant meaning and the low spans fail to maintain the subordinate meaning. As a result, on encountering the disambiguating information, the two groups are in their different knowledge states.

3.5. Low spans and disambiguating information

When low span readers encounter the disambiguating information after a balanced ambiguity, they are in one of three possible states: (1) both meanings are available but they have not committed to an interpretation, (2) they have an interpretation for the more frequent meaning and have the less frequent meaning available, or (3) they have both interpretations available. Any of these possibilities creates processing demands for low span readers such that they have to activate the right hemisphere homologues of the language areas to compensate. For biased ambiguous words, low span readers most likely only have the dominant meaning and interpretation available. This creates a problem when they encounter a

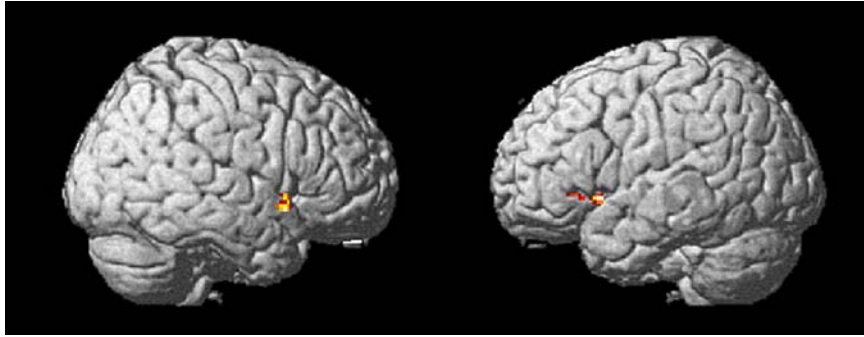


Fig. 2 – The bilateral insula activation is shown from the subtraction of sentences containing biased ambiguous words minus sentences containing balanced ambiguous words. Activation is projected onto the surface rendering. The corresponding cortical regions, cluster sizes, peak *T*-values and MNI coordinates can be found in Table 1.

sentence that is disambiguated to the subordinate meaning. As a result, prefrontal regions become active in response to the incoherence (Ferstl and von Cramon, 2001, 2002) and some right temporal activation appears in response to the possibility that some residual activation remains on the coarse-coded subordinate meaning.

3.6. High spans and disambiguating information

When high span readers encounter the disambiguating information after a balanced ambiguity, they most likely have both interpretations available, reducing the difficulty of processing. On the occasions in which high spans do not have both interpretations available, they at least have the meanings available or simply have to recruit the right hemisphere to support the construction of the alternate interpretation. This set of circumstances combined with the low spans' need to recruit the right hemisphere contributes to the finding of the right hemisphere activation in the overall ambiguity effect across groups. For the biased ambiguous words, the high span readers most likely have committed to the dominant meaning but have the subordinate meaning available. In response to the subordinate meaning, they may find little difficulty in constructing the alternate interpretation; however, they may have to actively suppress the dominant interpretation as was indicated by the insula activation. This is not a novel idea, Gunter et al. (2003) have proposed that high span individuals use inhibition in a more flexible manner than do low spans.

Clearly, this account is speculative and should be viewed as an early step in the process of understanding how lexical ambiguities are processed in context. Much as behaviorally based accounts have developed over many experiments, so too must an accurate account of the cortical network underlying this language process.

4. Experimental procedure

4.1. Participants

The participants were 12 right-handed paid volunteer college students (3 females). Each participant gave signed informed

consent that had been approved by the University of Pittsburgh and Carnegie Mellon University Institutional Review Boards. Participants were familiarized with the scanner, the fMRI procedure, and the sentence comprehension task before the study started.

4.2. Materials

Many of the stimulus items were identical or modifications of sentences that have been used in various lexical ambiguity behavioral studies (Duffy et al., 1988; Miyake et al., 1994). Each sentence frame was constructed such that an ambiguous word or a matched control word appeared early in the sentence before any disambiguating context. The biased ambiguous sentence frames were always disambiguated to the subordinate meaning of the ambiguous word. Balanced ambiguous sentence frames were only disambiguated to one of the equally likely meanings of the ambiguous word. The full set of sentences can be found in the Appendix. Participants read a total of 36 sentences, 9 sentences in each of 4 conditions in the study. Participants were assigned to one of two groups and the ambiguity of a sentence was varied across groups. There was no effect of material set on the activation data so the analysis was collapsed across groups.

The inter-sentence intervals were filled with a 12-s rest period, consisting of a centered “X”, to allow the hemodynamic response to approach baseline between sentences. At two equally spaced intervals during the task, the 12-s rest period was extended to 30 s for one inter-sentence interval. Additionally a 30-s rest period occurred at the beginning and end of the experiment. These fixation periods were not necessary for the analysis described below but were included to allow for possible additional analyses.

4.3. Stimulus presentation

Sentences were presented one word at a time in a cumulative manner with the first word appearing on the left side of the screen approximately in the middle of the participant's vertical field of view. Each consecutive word appeared to the right of the previous word until a line was full, at which point a

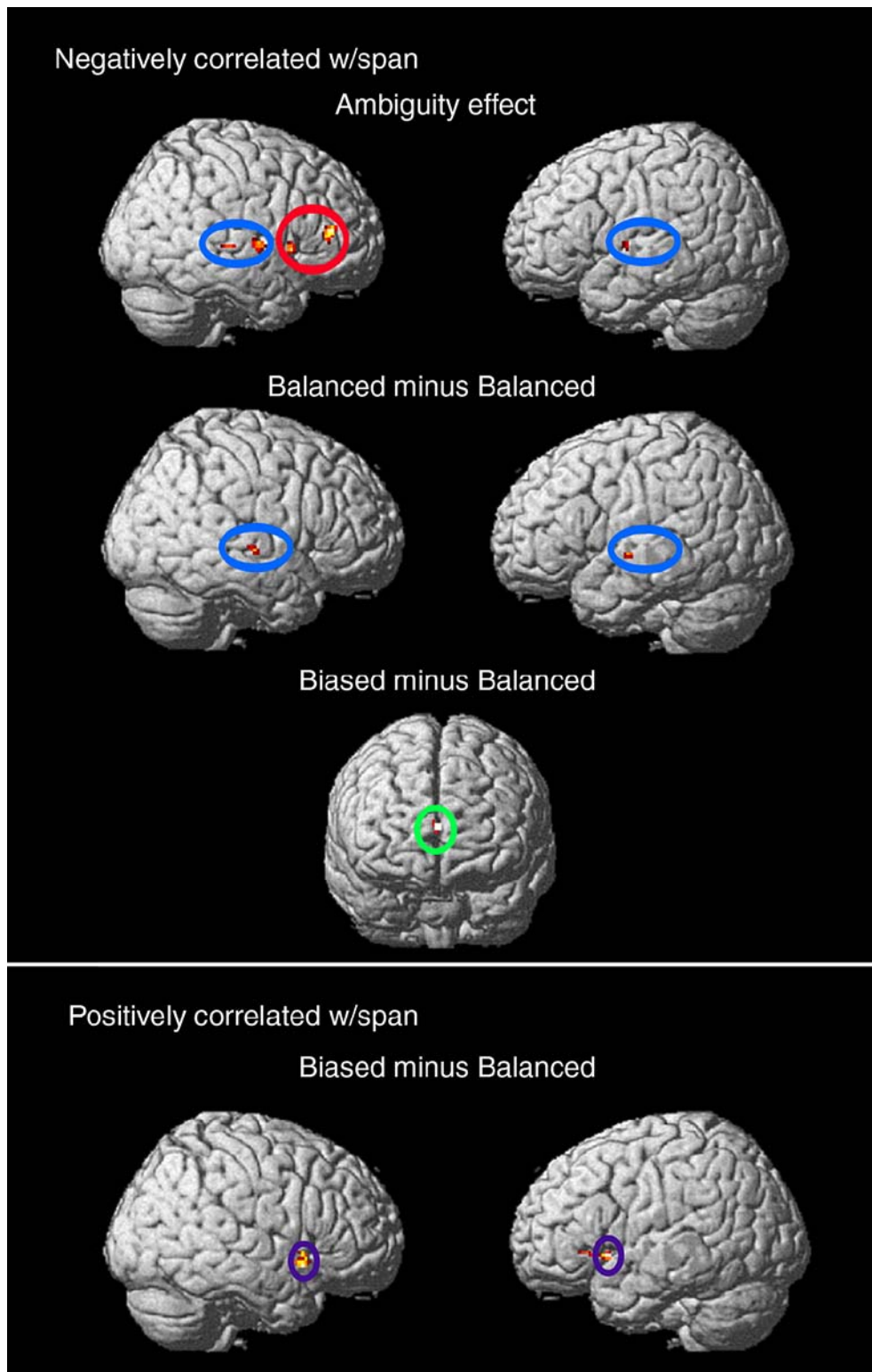


Fig. 3 – Activation maps for areas that were correlated with reading span for the ambiguity contrast as well as the direct subtractions between the two types of ambiguous words. The negatively correlated regions indicate that the readers with a lower RSPAN are more likely to use right IFG (circled in red), bilateral temporal (in blue) and medial frontal (in green). In contrast, bilateral insula (circled in purple) was the only region positively correlated with RSPAN.

second line was initiated. The words were presented at a rate of 300 ms per word plus an additional 16.67 ms per character. A similar rate had been previously used by [Gernsbacher \(1989\)](#)

and [Wiley et al. \(2001\)](#) in a variation of this procedure. The base 300 ms rate was decreased from a base 450 ms rate used in those studies in order to more closely approximate

Table 2 – Areas of activation that were significantly correlated with RSPAN

Cortical region	Cluster size	Peak T-value	MNI coordinates		
			x	y	z
(A) Ambiguity Effect – negatively correlated with span					
Right anterior cingulate	71	7.90	10	26	8
Right inferior frontal/middle frontal	57	5.04	40	38	10
Right inferior frontal	26	4.66	48	14	2
Right superior temporal/Heschle	41	4.62	52	-6	2
Right superior temporal	11	3.91	54	-28	2
Right putamen	15	3.76	30	-4	6
Left rolandic operculum	7	3.34	-48	-6	4
(B) Balanced Ambiguous – negatively correlated with span					
Right middle frontal	45	6.26	40	40	12
Right inferior frontal	9	4.16	56	34	8
Right superior temporal	14	3.87	56	-24	2
(C) Biased Ambiguous – negatively correlated with span					
Right superior temporal	65	6.50	54	-4	0
Right caudate	19	4.50	12	28	8
Left superior medial frontal/superior frontal	14	4.29	-12	48	16
Left caudate	38	4.22	-6	24	2
Right putamen	20	4.02	32	2	4
(D) Balanced versus Biased Ambiguous – negatively correlated with span					
Right superior temporal	9	6.01	66	-16	-2
Left middle/superior temporal	8	4.74	-62	-10	-2
(E) Biased versus Balanced Ambiguous – negatively correlated with span					
Right insula	50	6.14	42	12	-8
Left insula	20	4.58	-40	14	-6
Left inferior frontal	9	3.81	-42	26	-2
(F) Biased versus Balanced Ambiguous – positively correlated with span					
Left/Right medial frontal	18	3.57	0	64	12

The threshold for significant correlation was $p < 0.005$ for a spatial extent of at least 6 voxels, uncorrected for multiple comparisons. Region labels apply to the entire extent of the cluster. T-values and MNI coordinates are for the peak-activated voxel in each cluster only.

standard reading times.¹ The sentence remained on the screen for an additional 300 ms after all the words had appeared to allow for sentence wrap-up processing (Just and Carpenter, 1980).

¹ For example, Rayner (1978) showed that average fixation duration for college students reading light fiction was only 202 ms per word. Furthermore, even when participants used a button press to present the next word, the average time per word was “at least 400 ms” (from Rayner and Pollatsek, 1989 citing evidence from Aaronson and Scarborough, 1976; Aaronson and Ferris, 1983; and Just et al., 1982). Although it is a concern that this rate might affect low spans more than high spans (Poldrack et al., 2001), there was no correlation between error rates and RSPAN, nor were there any areas of activation that were correlated with RSPAN in additional analysis in which unambiguous sentence were contrasted with fixation.

A yes–no comprehension question immediately followed the sentence. Participants were told to respond as quickly as possible within a 4-s limit. Few failures to respond within the time limit occurred. After the participant answered the question or 4 s had elapsed, an “X” appeared on the screen for the rest period. The sentence presentation, probe presentation and response, and the 12-s rest that followed constituted between 20 and 23 s, depending on the total sentence presentation time and the question answering response time.

4.4. Scanning procedures

A seven slice oblique axial prescription (approximately 10° angle) was set that maximized the coverage of the middle to superior portions of the temporal lobe (STG, including Wernicke’s area) and the inferior frontal gyrus (IFG including Broca area). Fig. 4 shows the location of the slices for one of the participants. The onset of each ambiguous word within the sentence was synchronized with the beginning of the second acquisition of the superior most slice.

Cerebral activation was measured using blood oxygenation level-dependent (BOLD) contrast (Kwong et al., 1992; Ogawa et al., 1990). Imaging was done on a 1.5 T scanner at the MR Research Center at the University of Pittsburgh Medical Center. The acquisition parameters for the gradient-echo EPI with 7 oblique axial slices were TR=1.5 s, TE=50 ms, flip angle=90°, 128×64 acquisition matrix, 5 mm thickness, 1 mm gap, RF head coil. The structural images with which the functionals were co-registered were 124-slice axial T₁-weighted 3D Spoiled GRASS (SPGR) volume scans that were acquired in the same session for each participant with TR=25 ms, TE=4 ms, flip angle=40°, FOV=24 cm and a 256×256 matrix size.

4.5. Data analysis

To compare the participating groups in terms of the distribution of activation, the data were analyzed using both FIASCO and SPM99. First, the image preprocessing corrected for in-

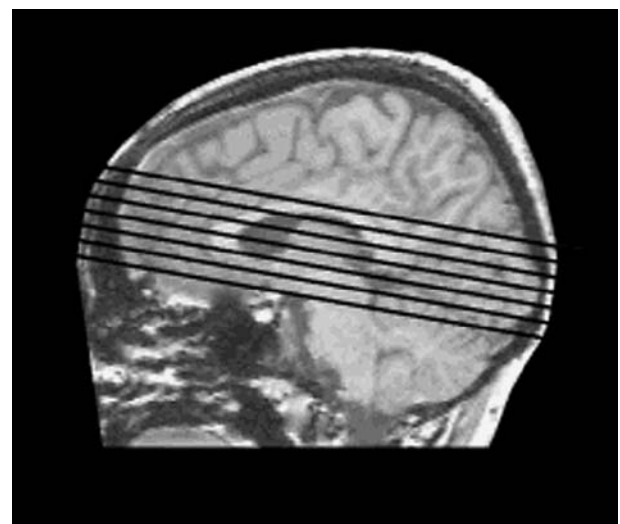


Fig. 4 – The slice prescription for a typical participant.

plane head motion and signal drift using procedures and the FIASCO software developed by Eddy et al. (1996). These preprocessed images were then corrected for slice acquisition timing, 3-D motion-corrected, normalized to the Montreal Neurological Institute (MNI) template, resampled to $2 \times 2 \times 2$ mm voxels, and smoothed with an 8-mm Gaussian kernel to decrease spatial noise. For the activation maps, statistical analysis was performed on individual and group data by using the general linear model (GLM) and Gaussian random field theory as implemented in SPM99 (Friston et al., 1995). For the GLM, a separate regressor was specified for each of the four sentence types. For each sentence within a condition, a base hemodynamic response function was convolved with a boxcar function; the onset of this boxcar was the time point at which a sentence appeared on the screen and the duration of the boxcar equaled the duration of the sentence. For the random effects analysis on group data, one-sample t-tests were performed on contrast images obtained from each individual analysis. Activated brain areas

surviving an uncorrected height threshold of $T=3.11$ ($p=.005$) and an extent threshold of 6-mm^3 voxels were rendered on a template brain in SPM.

4.6. fMRI analyses: Correlation of RSPAN with the distribution of activation

Whole-brain simple correlation was used to examine the relationship between out-of-magnet reading span (RSPAN) and the magnitude of cortical activation during sentence processing. In these analyses, the dependent measure at each voxel was the participant's first-level contrast value for the various contrasts across sentence type, and the independent variable was the participant's RSPAN score. The correlation with brain activation was calculated at each voxel, and the t-maps testing the difference of this parameter estimate from zero were thresholded at $p < 0.005$, uncorrected, extent threshold = 6 voxels. This probability map therefore shows areas where there was a reliable correlation between RSPAN

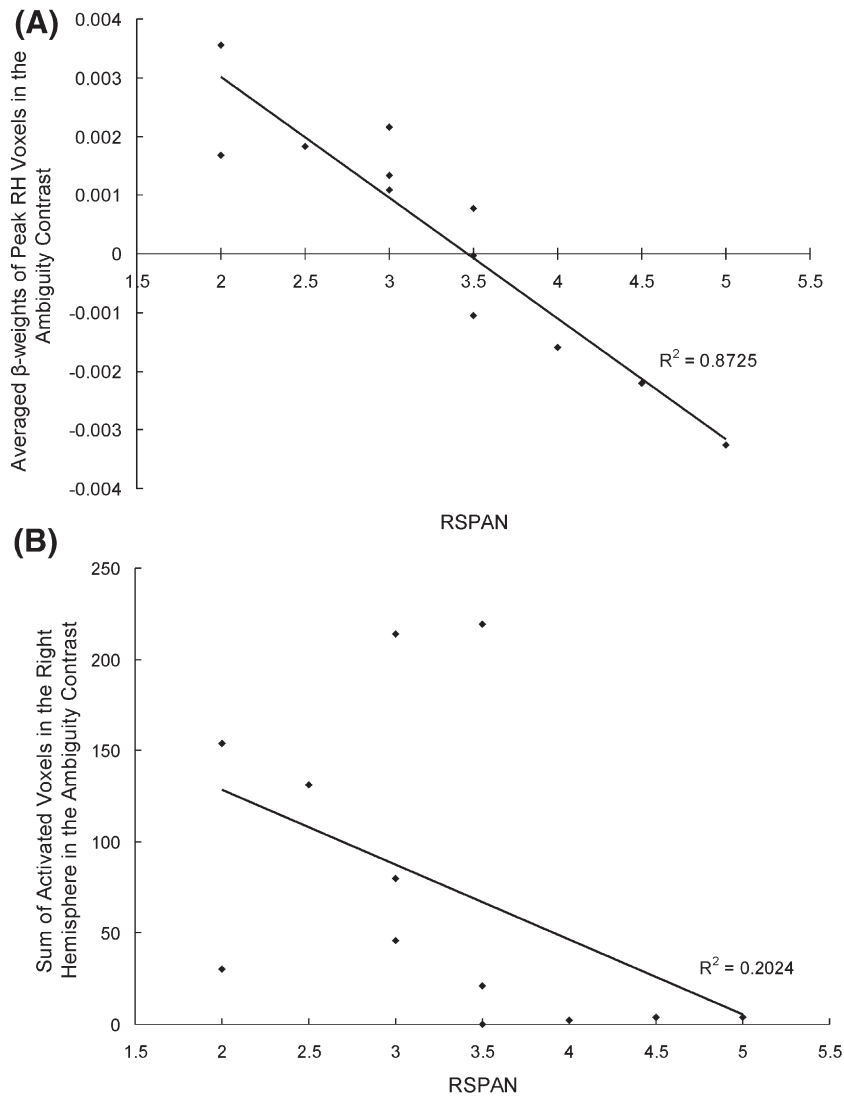


Fig. 5 – (A) A scatterplot showing the negative correlation between RSPAN and the β -weights corresponding to the peak right hemisphere voxels in clusters which correlate with RSPAN. **(B)** A scatterplot showing that the negative correlation is present in the volume of right hemisphere activated voxels in the ambiguity effect contrast.

and activation. RSPAN was assessed via the Daneman and Carpenter RSPAN task (1980) prior to participating in the fMRI portion of the experiment. A scatter plot of the RSPAN values and the average β -weights for the peak right hemisphere voxels in the Ambiguous–Unambiguous contrast is shown in Fig. 5A. As a converging measure, the scatter plot of the RSPAN values and the sum of all right hemisphere activation in the Ambiguous–Unambiguous contrast is presented in Fig. 5B. As can be seen, the spread of RSPANs across the 12 participants was large enough that correlation could be used in the distribution of activation analysis even though the majority of the participants had RSPAN scores in the mid-range.

5. Uncited references

Beeman and Chiarello, 1998
Mason et al., 2003

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Appendix A

Biased subordinate sentence frames (ambiguous word):

Actually the **soup (port)** was popular even though it had a strange flavor.

Q: Was the soup popular?

Unfortunately the **total (table)** was too large for him to copy it into his notebook.

Q: Did the total fit into the notebook?

The new **parkway (diamond)** was too small although they built according to plans.

Q: Did the construction company follow the plans?

Yesterday the **tenant (racket)** was unacceptable although he was impressed with the apartment.

Q: Did the landlord find the tenant acceptable?

Last year the **zoo (pen)** was abandoned because it was too dirty for the animals to live in.

Q: Was the zoo dirty?

Unfortunately the **edge (bank)** was rather dirty even though the town took care to keep the river itself clean

Q: Did the town work to keep the river clean?

Unfortunately the **gold (band)** was lost after it suddenly fell off her finger.

Q: Was the gold lost?

Last night the **sword (poker)** was abandoned after it accidentally fell into the fire.

Q: Was the sword placed carefully into the fire?

Last year the **jail (mint)** was well advertised because it was hiring twenty new employees.

Q: Was the jail hiring forty new employees?

This time the **tale (yarn)** seemed new even though he had read it many times before.

Q: Was the tale being read for the first time?

Last night the **stone (scale)** was taken away to be analyzed after it was carefully removed from his throat.

Q: Was the scale removed from his throat?

Now the **hair (bill)** was not quite right although the head of the animal had been well sketched.

Q: Did the animal have a bill?

This time the **test (ball)** was moved because it was always so well attended.

Q: Was the ball always well attended?

At last the **tourist (cabinet)** was finished after attentively listening to the president's speech.

Q: Was the vice-president giving a speech?

Yesterday the **puppy (boxer)** was miserable after its hind legs were injured in the accident.

Q: Was the dog's hind legs injured?

Unfortunately the **cabin (coach)** needed air-conditioning because it was always too hot to sleep in.

Q: Did the coach need air-conditioning?

Yesterday the **tail (horn)** was mounted on the wall after it was cut off the dead animal.

Q: Was the horn mounted today?

Today the **pope (wire)** was received with smiles because he (it) brought such good news.

Q: Did the message bring bad news?

Balanced sentence frames (ambiguous):

Of course his **face (case)** attracted attention although it was wrinkled and worn.

Q: Was his face wrinkled?

Last month his **flesh (chest)** was discolored since it had been bruised in a fight.

Q: Did he escape the fight unscathed?

He found the **meat (mold)** in the garbage can after smelling something strange in the kitchen.

Q: Was the meat found in the refrigerator?

To their surprise, the **howl (bark)** was unusual because it sounded high-pitched and hoarse.

Q: Was the noise high pitched?

Today the **nurse (pupil)** was rather wet after waiting in the rain for the bus.

Q: Was it raining outside?

Of course the **desk (cell)** looked small because it was piled high with supplies.

Q: Was the desk empty?

Today the **fence (panel)** finally gave in after warping and sagging for months.

Q: Is the fence still standing?

Last week the **chalk (ruler)** was missing although she had been careful to put it away.

Q: Was the chalk where she put it away?

Unexpectedly the **film (date)** was awful even though she had been looking forward to it for a week.

Q: Was she looking forward to the film?

Last year the **skit (deed)** was widely publicized because everyone agreed it was so well performed.

Q: Was the deed publicized last year?

Of course the **whiskey (pitcher)** was often forgotten because it was kept on the back of a high shelf.

Q: Was the pitcher used often?

This morning the **cook (cast)** was in bad shape after spending most of the night celebrating.

Q: Did the cast celebrate last night?

Not surprisingly, the **woman (board)** looked old and weathered after a year in the hot southern sun.

Q: Did the sun damage the wood?

He decided the **yard (gate)** would be fine after spending his summer vacation designing it.

Q: Did he hire someone to design his yard?

At last the **pan (fan)** was in good shape once its broken handle had been repaired.

Q: Was it a pot that was repaired?

Sighting the **airplane (cardinal)** was exciting after searching the sky for hours.

Q: Was the bird sighted?

Yesterday the **ashes (straw)** seemed wet although he had raked it into the barn early.

Q: Did the straw seem wet?

Unfortunately the **flute (spade)** fell to the floor after he played it with a great flourish.

Q: Did he play a heart?

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