

Bilateral brain processes for comprehending natural language

Mark Jung-Beeman

Department of Psychology, and Cognitive Brain Mapping Group, Northwestern University, 2029 Sheridan Road, Evanston, IL 60208-2710, USA

Comprehension of natural language – stories, conversations, text – is very simple for those doing the comprehending and very complex for cognitive neuroscientists. It also presents a paradox: the advantage of the left hemisphere (LH) for most language tasks is one of the best-established facts about the brain; yet, when it comes to comprehending complex, natural language, the right hemisphere (RH) might play an important role. Accumulated evidence from neuropsychology, neuroimaging, and neuroanatomy suggests at least three roughly separable (but highly interactive) components of semantic processing. Each process in turn has bilateral components, with the RH component performing coarser computations for the same general process. Examining asymmetrical brain and cognitive functions provides a unique opportunity for understanding the neural basis of complex cognition.

Introduction

How do people comprehend ‘natural language’ like stories, texts, and conversations? It’s a complex behavior, calling upon numerous cognitive and neural systems. A great deal of research has focused on how people decode written and spoken input into words, retrieve word meanings, and parse syntax. For over a century, the consensus has been that frontal and temporoparietal regions of the left hemisphere (LH) are crucial for these fundamental language processes. Investigating how the brain converts a continuous stream of words into meaningful communication has proceeded more slowly, but recent research is beginning to reveal how the brain comprehends natural language. One preliminary conclusion is that, as language input gets increasingly complex, there is increasing involvement of anterior temporal regions and of right hemisphere (RH) homologues [1–4] to classic LH language areas.

Several lines of evidence suggest that in addition to well-known LH language processing, the RH also contributes to language comprehension. First, qualitatively different semantic processing is manifest in distinct patterns of sensitivity to various semantic relations for words presented to the LH or RH of healthy subjects, via the right or left visual hemifield (rvf-LH or lvf-RH). Second, some patients with RH brain damage have subtle

deficits in comprehending natural language (reviewed in [3,5]). Third, neuroimaging studies often reveal neural activity in the RH during language tasks. Hundreds of neuroimaging studies reveal strong neural activity in the LH during language tasks [1–4]; but many of these studies also observe weak signal in homologous (anatomically equivalent) areas of the RH [2,3]. Moreover, a growing number of studies report RH greater than LH brain activity while subjects perform higher-level language tasks, such as comprehending metaphors [6–9], getting jokes [10,11], deriving themes [12], and drawing inferences [13], generating the best endings to sentences [14] mentally repairing grammatical errors [15], detecting story inconsistencies [16], and determining narrative event sequences [17]. This is not to say that the RH performs all the above functions, but it appears to contribute to them, at least in some circumstances.

Fourth, the RH can (sometimes) support language recovery. For instance, children with early brain damage [18], even those who have their entire LH removed (to treat epilepsy) during early adolescence [19], can recover most language abilities. Some (not all) adult patients who recover from aphasia (due to LH brain damage) show concomitant increased processing in homologous areas of the intact RH [20–22]. It is unlikely that patients grow new language areas in the RH; it seems more likely that RH language areas can become more finely tuned to perform tasks normally better performed by the LH. Finally, information processing is supported by neural substrates, and the two hemispheres are anatomically more similar than different. There are size asymmetries in some language areas, but there don’t appear to be cortical areas or pathways that are present in the LH but absent in the RH. The known asymmetries might correlate with language function, but not perfectly [23,24]). By contrast, at the microanatomical level, there are numerous asymmetries [25] that could support distinct computations (see Box 1) within a process, conferring distinct advantages to each hemisphere.

Semantic processing in natural language: *Bilateral Activation, Integration, and Selection (BAIS)*

Given the above evidence, a plausible account of how the brain supports natural language comprehension must consider hemispheric differences in language-related processes. In this article, I delineate a framework of multiple bilateral semantic processes that cooperatively

Corresponding author: Jung-Beeman, M. (mjungbee@northwestern.edu).
Available online 7 October 2005

Box 1. Coarseness of coding and neural microcircuitry

More than a metaphor, the term ‘coarse semantic coding’ is intended to spur investigation into the neural and computational bases of language asymmetries. Hemispheric studies are useful for linking wiring patterns to cognition generally, because the two hemispheres and their functions are more alike than different, making it potentially easier to relate wiring patterns to cognitive processes.

Both hemispheres process semantic information in highly distributed networks [63]. I propose that the evidence points to RH processing being more coarsely tuned than LH processing, because a greater spread of inputs and outputs in RH semantic areas produces more diffuse semantic activation, compared with homologous LH semantic areas. This view is consistent with data suggesting that the RH is generally more interconnected than the LH (for review, see [5]): Compared with the LH, the RH has a greater proportion of white matter (i.e. connections between neurons), a higher correlation of activity across regions, more diffuse electrophysiological responses, and more diffuse functional (e.g. motoric) deficits consequent to similar sized brain lesions.

This view is also consistent with asymmetries in cortical microcircuitry of language areas that influence how neurons spread information [5,25,64]. For example, at the cellular level, pyramidal

cell dendrites branch further from the soma and ultimately into more branches with more dendritic spines, on average, in the RH than in the LH. Such circuitry favors more input from relatively distant sources in the RH, and from close sources in the LH [25].

Because functional and structural levels of brain organization are interdependent, some effects at each level get passed through to higher levels. Thus, cortical mini-columns, macro-columns, and functional areas are more highly overlapping and more densely interconnected in the RH than in the LH [65]. Overall, these microcircuitry asymmetries suggest broader input and projection fields, and greater functional overlap across processing units in the RH than in the LH – precisely the conditions that should foster coarser coding.

It is a huge leap from dendritic branching to natural language comprehension; but cognitive asymmetries exist in language processing, microcircuitry asymmetries exist in language areas, and semantic processing clearly requires neural activity. Moreover, coarse coding (population or vector coding) is well studied, neurally and computationally, in many domains. Therefore, I hope such an explanation of complex language asymmetries will lead to scrutiny at the neural and computational levels.

construct meaning from natural language. Here, the term semantic is used broadly, to denote any function pertaining to the extraction and elaboration of meaning from language input, rather than in the more restrictive sense often intended in linguistics. The framework is organized around two basic principles:

- (1) At least three distinct but highly interactive components of semantic processing, supported by three separable brain areas, are crucial for natural language comprehension: *semantic activation*, *semantic integration*, and *semantic selection* (see Figure 1). There could well be additional semantic processes or subprocesses, but these three provide a substantive part of the language comprehension network.
- (2) Each type of semantic processing occurs bilaterally, but – perhaps owing to neural microcircuitry (see Box 1) – the hemispheres compute information differently, such that the RH performs relatively *coarser semantic coding*. LH semantic coding is still

highly distributed (not localist), but is relatively fine compared with that of the RH.

These complementary RH and LH processing streams described in (1) interact, but each performs its own computation at every processing stage. The component processes in (2) are highly interactive. In the real world, it is unlikely that any one of these would ever be engaged in isolation of the other two. In the laboratory, the best we can do is to contrast tasks that tip the balance of processing towards one process or another. In the following, I present evidence for each of these putative semantic processes, and their bilateral nature.

Semantic activation in posterior middle temporal gyrus

When people encounter words, they think about, or activate, information related to each input word. ‘Semantic activation’ provides initial access to semantic representations (which are themselves distributed), activating features and first-order associations of the input word. Based on lesion and neuroimaging data [2–4], semantic activation depends largely on bilateral Wernicke’s areas – especially posterior middle and superior temporal gyri (MTG, STG). Related processes might be supported by angular and supramarginal gyri [26], and perhaps inferior temporal lobe [27], with distinct areas important for different modalities of input and characteristics of information.

The information activated in response to input can be termed a ‘semantic field’, analogous to a sensory receptive field (although it is actually a projective field). According to the current framework, each input word elicits a semantic field in each hemisphere, a strongly focused one in the LH and a diffuse one in the RH (see Figure 2). The two hemispheres probably store similar representations, but differ in the way they dynamically access information. The semantic fields activated in response to input are shaped by context, and each hemisphere is particularly sensitive to different contexts, and differently modulated by attention and time course.

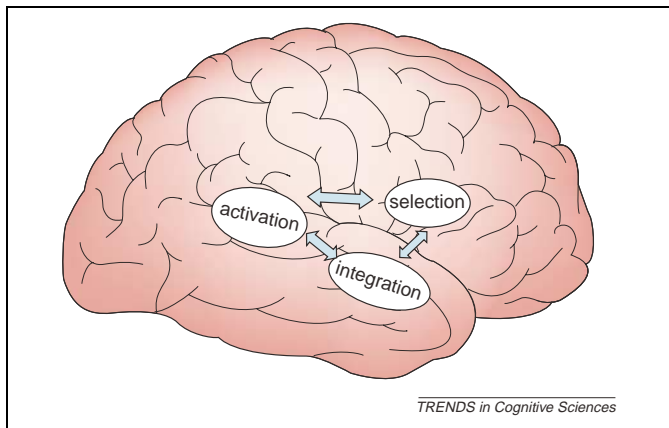


Figure 1. Three component semantic processes that contribute to natural language comprehension: semantic activation, in posterior middle/superior temporal gyri; semantic integration, in anterior middle/superior temporal gyri; and semantic selection, in inferior frontal gyrus. The three components are proposed to have counterparts in both hemispheres (i.e. a RH and a LH version of each process), and to interact across processes and across hemispheres.

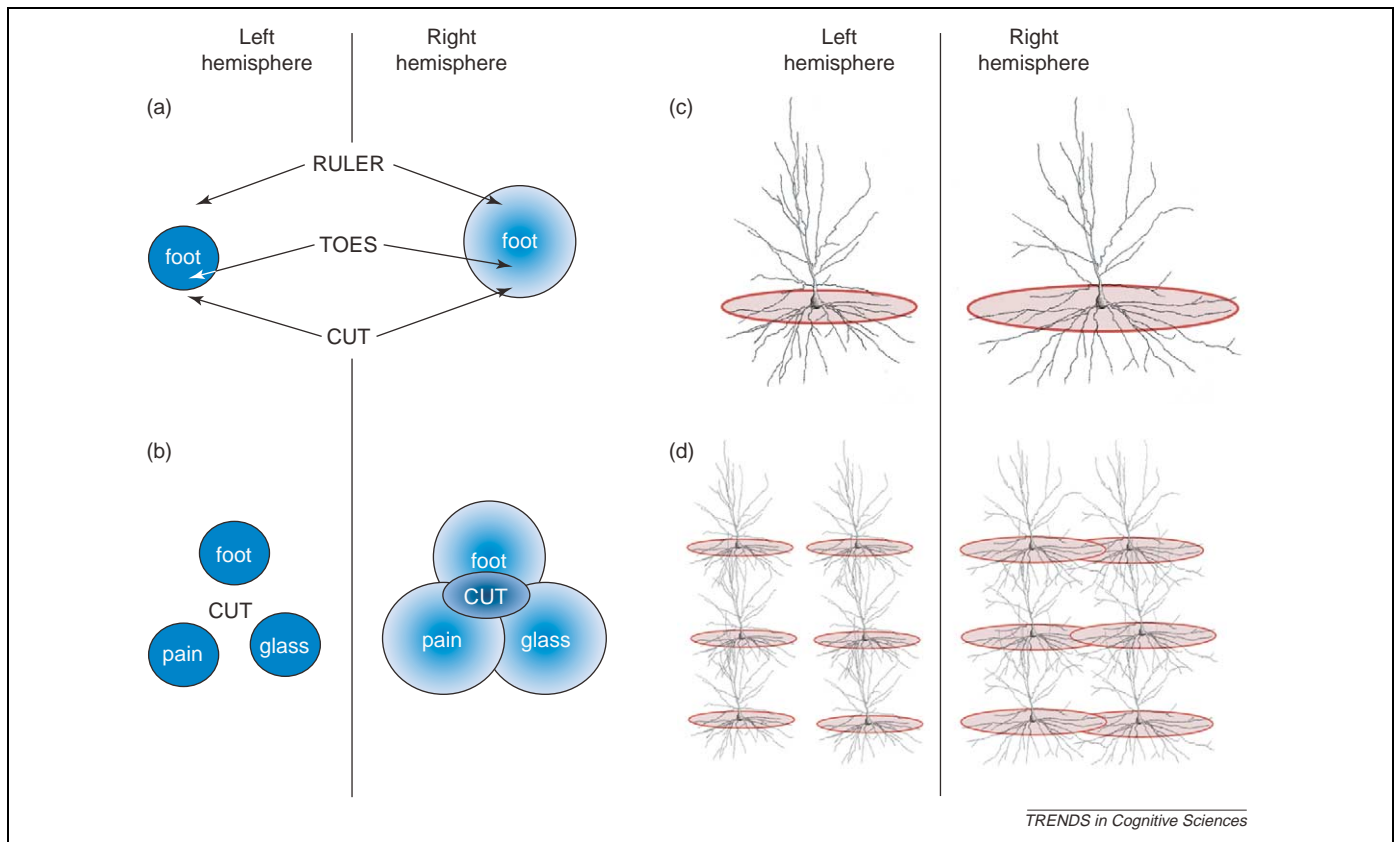


Figure 2. (a) The LH strongly activates small and focused semantic fields, containing information closely related to the dominant meaning of input word(s). By contrast, the RH weakly activates large diffuse semantic fields, including information distantly related to the words, providing only a coarse interpretation, insufficient for many language tasks. (b) However, the larger semantic fields of the RH are more likely to overlap, allowing weak activation to summate, when input includes multiple distantly related words. Therefore, the RH is sensitive to distant semantic relations, and comprehenders capitalize on this sensitivity when understanding natural language, particularly figurative language or unusual constructions. (c) Neurons in RH and LH language areas differ in several characteristics likely to affect computations; for example, pyramidal neurons in the RH have longer initial dendritic branches and more synapses further from the soma, on average, than LH neurons. This causes RH neurons to receive a broader and more overlapping field of inputs than those of the LH (see also Box 1; [51]) (Figure adapted with permission from [68].) d. LH cortical columns are more widely spaced than RH cortical columns, with less overlap among input fields.

Ultimately, the LH quickly focuses semantic activation on features related to the dominant, literal or contextually relevant meaning while inhibiting features related to the subordinate or contextually irrelevant meanings. This strong categorical semantic activation is conducive to most language comprehension tasks, and especially to production – speakers must produce a single word, not a hybrid of several related ones. By contrast, the RH maintains weak, diffuse semantic activation of a broader semantic field, including distant and unusual semantic features, features that seem irrelevant to the context, and secondary word meanings [28–32]. These large semantic fields provide only a coarse interpretation, rife with ambiguity. For instance, if you were listening to a story and heard the word ‘*foot*’, but couldn’t determine whether it referred to twelve inches or a part of the body, you would quickly get bogged down, unable to follow rapidly unfolding natural language.

However, coarse semantic activation has some advantages. Given multiple input words, larger semantic fields are more likely to overlap than smaller, more focused semantic fields. Thus, the RH is more sensitive than the LH to distant semantic relations, as observed when people make semantic relatedness judgments to words presented to the rvf-LH versus the lvf-RH [31]. People also show stronger semantic priming (i.e.

facilitated responses) in the lvf-RH than in the rvf-LH for target words that are distantly related to preceding prime words, but stronger priming in the rvf-LH for target words closely related to the preceding primes [28–30,32]. Event related potentials (ERPs), particularly when paired with visual hemi-field presentations, also demonstrate hemispheric differences in semantic processing [33]. Reduced N400 amplitude (indicating semantic relatedness) to lvf-RH target words indicates the RH is particularly sensitive to: feature overlap in the absence of associations [34]; indirect (i.e. mediated) semantic relations [35]; unusual interpretations [36]; and joke endings [10,28].

The biggest advantage conveyed by coarse semantic coding arises when people process multiple distantly related words, as in natural language. On a smaller scale, when people view three-word primes (*foot-glass-pain*) where each word is distantly related to a target word (CUT), weak semantic activation from the three prime words appears to summate in the RH, yielding stronger priming for lvf-RH than for rvf-LH target words. By contrast, a single strongly related prime word (*scissors*) yields stronger priming for rvf-LH than for lvf-RH target words [37]. Such crossover interactions demonstrate qualitative rather than quantitative differences in semantic processing.

When understanding natural language, larger semantic fields could include information that initially seems irrelevant, but which turns out to be important. Thus, coarser semantic activation sets the stage for the RH to contribute uniquely to natural language comprehension. Although semantic activation initiates processing, semantic integration and selection rapidly interact, elaborating on the initial processing asymmetries.

Semantic integration in anterior temporal lobes

'Semantic integration' supports message-level interpretation by computing the degree of semantic overlap among multiple semantic fields. A host of results support the contention that semantic integration depends on bilateral anterior (anterior to primary auditory cortex) superior temporal gyrus (STG) and superior temporal sulcus (STS), extending into middle temporal gyrus (MTG) and temporal pole (although that area can be difficult to image with fMRI). Semantic integration in this anterior temporal area (hereafter aSTG) detects, elaborates, and refines higher order semantic relations.

This is the most controversial of the three processes (see also Box 2), and a good example of how neuroimaging data can inform cognitive theory. It is hypothetically possible that semantic activation and semantic integration could be served by a single cortical area, but the evidence – limited though it is – suggests otherwise. When people process meanings of isolated words, activity increases in posterior temporal cortex. When people comprehend (read or listen to) sentences or stories, neural activity increases in aSTG or temporal pole, bilaterally [1,2,16,38–40].

When people perform tasks emphasizing semantic integration, neuroimaging signal can be predominantly right-sided [12], and patients with RH brain damage (with an intact LH) can have selective difficulties – they do not appear aphasic, but may miss the gist of stories or conversations (reviewed in [5]). Consider how people derive and use story themes. When comprehending stories, the title gives people a framework for understanding the passage. Omitting the title removes a link between distantly related story elements, so comprehension requires more semantic integration, and in such conditions subjects show increased neural activity in

the anterior temporal lobe in the RH, and decreased activity in some homologous LH regions [12]. Also, when people detect information inconsistent with the global context (e.g. a change in character emotion, or a violation of temporal order), neural activity increases in right anterior temporal lobe [16]. Similar RH areas are active when people mentally repair grammatical errors in sentences, requiring construction of new semantic relations [15], or when they generate the 'best ending' to a sentence [14]. These results echo the difficulties (reviewed in [5]) that some RHD patients have understanding or deriving the theme of stories, organizing sentences into stories, recalling connections between story elements, and mentally rearranging words in a sentence.

Drawing causal inferences also requires semantic integration. Most people, when hearing the following excerpt: '*Samantha was walking on the beach in bare feet, not knowing there was glass nearby... Then she felt pain, and called the lifeguard for help*', would infer that she cut her foot. When healthy subjects comprehend stories that imply causal events, inference-related semantic priming is found earlier in the lvf-RH, and later in the rvf-LH, suggesting that the hemispheres play complementary roles in drawing connective inferences [41]. Some RHD patients have difficulty drawing such inferences [42], and do not show inference-related priming [43]. Moreover, when people read sentence pairs requiring inferences, the pattern of fMRI signal in RH STG resembles patterns of behavioral responses thought to indicate inferencing [13]. However, some studies fail to observe RH-specific neural activity when people process text that encourages inferences [44].

Comprehending figurative language places particular demands on semantic integration, and could be aided by processing in RH temporal cortex [3]. For instance, metaphors capitalize on distant semantic relations between words, especially metaphors that are more novel, more creative, and less salient. Metaphors can be difficult for some patients with RH brain damage to process [45]. Healthy people show semantic priming of metaphors meanings more consistently when responding to lvf-RH than to rvf-LH target words [46,47]. Some studies [6–9] reveal neural activity in RH temporal cortex when people comprehend metaphors, although other

Box 2. Semantic integration: why, and why here?

Why is semantic integration a separate cognitive process, requiring a distinct cortical area? Ultimately, these are empirical questions, and available data indicate that anterior temporal areas are involved in semantic integration and posterior temporal areas are involved in semantic activation. One possible advantage of an additional brain area dedicated to semantic integration is that, like the 'hidden layer' in neural networks, it might facilitate recognition of higher-order semantic relations – relations that depend on other relations. For example, two concepts not directly related to each other might generally be 'related' because they share some other relations in common: either because both are related to similar concepts, or because they are both linked to a single concept within a story.

Also, a distinct brain region supporting semantic integration could allow the brain to refine, elaborate and select integrative concepts. Complex semantic relations are important for communication, and a dedicated brain region would allow such information to be attended,

selected, elaborated and manipulated to improve our understanding. Analogously, all the information about visual motion is embedded within neural responses in primary visual cortex, but an additional brain area elaborates processing about visual motion.

Inferior temporal lobe is important for visual processing and STG for auditory processing, so STS and MTG might be ideally placed to integrate across modalities. In fact, STG and MTG each have cortical patches receiving inputs from one sensory modality located very near patches receiving inputs from other modalities, and between these are still other patches that respond to multimodal stimuli [66]. It has been argued [64] that the long intrinsic connections in STG – outside primary auditory cortex – are well-suited to integration across processing areas; these connections are longer in the RH than in the LH [64]. It could be that semantic processing becomes increasingly complex and hierarchical from posterior to anterior STG/MTG, just as proposed for visual processing along inferior temporal cortex [67].

studies show stronger activity in the LH (e.g. [48]). Thus, RH semantic processing appears to contribute to understanding metaphors, a creative aspect of language comprehension. Creative problem solving, such as solving verbal problems with insight, also seems to benefit from RH semantic processing and particularly RH aSTG [49–51].

Another view suggests that RH semantic processing is integrative, whereas LH semantic processing is predictive, narrowing the scope of expectations of upcoming input [13]. However, the RH seems particularly sensitive to concepts that support predictive inferences [41], and it is possible that apparent differences in predicting information are related to coarseness of semantic activation and integration. Some components of discourse processing require tight semantic integration, and could depend heavily on LH processing; I have emphasized RH contributions because they are less well known. Other aspects of discourse processing may depend on what linguists refer to as pragmatics rather than semantic processing, strictly defined; but it is parsimonious to account for as much language comprehension as possible with relatively bottom-up semantic processing, broadly defined. Anatomically, some areas of aSTG are seemingly involved in other functions, although some appear to be integrative in their own right [52].

Despite these caveats, the consensus evidence is consistent with the possibility that bilateral aSTG supports semantic integration, more coarsely in the RH than in the LH. Semantic integration extrapolates on asymmetries in semantic activation, providing integrative concepts that could be selected, and can also operate on selected concepts to construct complex representations of natural language.

Semantic selection in inferior frontal gyrus

‘Semantic selection’ is the interactive process by which competing activated concepts are sorted out, inhibiting competing concepts while selecting one concept for action (including but not limited to response production), or for consciousness. Selection modulates word-level semantic activation and message-level semantic integration. There is strong evidence that semantic selection depends on the inferior frontal gyrus (IFG). Indeed, it has been proposed that the IFG performs selection more generally, with semantic selection being just one aspect [53–58].

Many semantic tasks evoke neuroimaging signal in the left IFG, and patients with damage in the left (or bilateral) IFG can have subtle deficits in semantic processing. IFG has variously been proposed to be important for directing semantic retrieval [59]; semantic decision-making and executive processes [3]; and semantic selection [53,57]. Semantic selection, broadly conceived, seems the best candidate to subsume the other putative processes – for instance, highlighting concepts during directed semantic retrieval. It also is highly likely that multiple functions are supported by IFG; at the least, different portions of this large gyrus could support several related – or unrelated – functions.

The degree that tasks require rapid selection among competing representations, for semantic decisions or output, is strongly associated with the degree of IFG activity, usually in the LH (reviewed in [54]). This is consistent with relatively finer semantic coding in the LH, because strong and focused semantic fields are more conducive to selection than diffuse semantic fields; if left IFG engages in relatively fine semantic selection, then it should have a double advantage in selecting concepts, compared with right IFG. However, there is some evidence that IFG in the RH is important for tasks requiring selection [60], particularly when information to be selected is more strongly activated in the RH than in the LH [17,61]. For instance, when people are given a common noun (e.g. *cake*) and asked to produce a typical use (*‘bake’* or *‘eat’*), the left IFG is strongly active; but when asked to produce an unusual use (e.g. *‘sell’*) of such nouns, the right IFG is more strongly active [62].

Altogether, evidence suggests bilateral components of IFG to be involved in semantic selection or some closely related process, allowing comprehenders to select concepts – given by the text or derived through integration – for output or to build their mental representation of natural language input.

Conclusions and future directions

Evidence from cognitive neuroscience is approaching a critical mass of data regarding the neural bases of natural language comprehension. Current data support a biologically plausible model with at least three semantic processes, each with components in both hemispheres – bilateral activation, integration and selection (BAIS). These components comprise a bilateral network of highly interactive semantic processing to interpret input and

Box 3. Questions for future research

- Are there multiple components of semantic activation, perhaps modality specific, in and around Wernicke’s area? Some evidence suggests that inferior temporal, supramarginal, and angular gyri may be important for semantic processing.
 - Is semantic integration different from *‘incorporation’* proposed by classic models of text comprehension? It seems likely that the behavior described as incorporation – integrating the main propositions of the text into a coherent representation – would occur within the network described here, emphasizing semantic integration to construct representations, rather than to process input.
 - Are there multiple components within inferior frontal gyrus (IFG)? Even studies purportedly demonstrating that IFG performs selection

show multiple loci of involvement, and also show strong involvement in the ‘no selection’ condition – just not as much as in the selection condition.

- What is the precise role of the medial frontal gyrus (MeFG) in detecting, maintaining, or building coherent natural language representations [21]. Do right and left MeFG compute coherence differently, but more coarsely in the right?
 - Does the RH participate in all language processes, even syntax, in each case computing information more coarsely than does the LH?
 - When and how do hemispheres share information, and when and how do they maintain different semantic processes?

organize representations of natural language. These qualitative differences allow a two-pronged approach to natural language comprehension: rapid interpretation and tight links in the LH, and maintenance of broader meaning activation and recognition of distant relations in the RH. Future studies should further specify the precise nature of these putative components, additional processes responding to natural language coherence [16,44] or other forms of semantic activation, as well as the interaction between these and other language, and general cognitive, processes (see Box 3). Finally, it is time to integrate the basic findings of hemispheric asymmetries in neural microcircuitry [25] with those of complex cognitive processes, because differences in microcircuitry must have computational implications, and asymmetries in language function must emerge from a neural substrate.

Acknowledgements

I wish to thank many colleagues and several anonymous reviewers. Thanks also to Jeffrey Hutsler for providing the basis for Figure 2c. This paper was written while the author was supported by grant DC04052 from the National Institute of Deafness and Communication Disorders, the National Institutes of Health.

References

- Humphries, C. *et al.* (2001) Role of anterior temporal cortex in auditory sentence comprehension: an fMRI study. *Neuroreport* 12, 1749–1752
- Xu, J. *et al.* (2005) Language in context: emergent features of word, sentence, and narrative comprehension. *Neuroimage* 25, 1002–1015
- Bookheimer, S. (2002) Functional MRI of language: New approaches to understanding the cortical organization of semantic processing. *Annu. Rev. Neurosci.* 25, 151–188
- Demonet, J-F. *et al.* (2005) Renewal of the neurophysiology of language: Functional neuroimaging. *Physiol. Rev.* 85, 49–95
- Beeman, M. (1998) Coarse semantic coding and discourse comprehension. In *Right Hemisphere Language Comprehension: Perspectives from Cognitive Neuroscience* (Beeman, M. and Chiarello, C., eds), pp. 255–284, Erlbaum
- Bottini, G. *et al.* (1994) The role of the right hemisphere in the interpretation of figurative aspects of language: A positron emission tomography activation study. *Brain* 117, 1241–1253
- Mashal, N. *et al.* An fMRI investigation of the neural correlates underlying the processing of novel metaphoric expressions. *Brain Lang.* (in press)
- Mashal, N. *et al.* The role of the right hemisphere in processing nonsalient metaphorical meanings: Application of Principal Components Analysis to fMRI data. *Neuropsychologia* (in press)
- Sotillo, M. *et al.* (2005) Neural activity associated with metaphor comprehension: spatial analysis. *Neurosci. Lett.* 373, 5–9
- Coulson, S. and Wu, Y.C. (2005) Right hemisphere activation of joke-related information: An event-related brain potential study. *J. Cogn. Neurosci.* 17, 494–506
- Goel, V. and Dolan, R.J. (2001) The functional anatomy of humor: Segregating cognitive and affective components. *Nat. Neurosci.* 4, 237–238
- St. George, M. *et al.* (1999) Semantic integration in reading: Engagement of the right hemisphere during discourse processing. *Brain* 122, 1317–1325
- Mason, R.A. and Just, M. (2004) How the brain processes causal inferences in text: A theoretical account of generation and integration component processes utilizing both cerebral hemispheres. *Psychol. Sci.* 15, 1–7
- Kircher, T.T.J. *et al.* (2001) Engagement of right temporal cortex during linguistic context. *Neuropsychologia* 39, 798–809
- Meyer, M. *et al.* (2000) Neurocognition of auditory sentence comprehension: event related fMRI reveals sensitivity to syntactic violations and task demands. *Brain Res. Cogn. Brain Res.* 9, 19–33
- Ferstl, E.C. *et al.* (2005) Emotional and temporal aspects of situation model processing during text comprehension: An event-related fMRI study. *J. Cogn. Neurosci.* 17, 724–739
- Knutson, K.M. *et al.* (2004) Brain activation in processing temporal sequence: an fMRI study. *Neuroimage* 23, 1299–1307
- Cohen, L. *et al.* (2004) Learning to read without a left occipital lobe: Right hemispheric shift of visual word form area. *Ann. Neurol.* 56, 890–894
- Vargha-Khadem, F. *et al.* (1997) Onset of speech after left hemispherectomy in a nine-year old-boy. *Brain* 120, 159–182
- Blank, S.C. *et al.* (2003) Speech production after stroke: the role of the right pars opercularis. *Ann. Neurol.* 54, 310–320
- Blasi, V. *et al.* (2002) Word retrieval learning modulates right frontal cortex in patients with frontal damage. *Neuron* 36, 159–170
- Leff, A. *et al.* (2002) A physiological change in the homotopic cortex following left posterior temporal lobe infarction. *Ann. Neurol.* 51, 553–558
- Gannon, P. *et al.* (1998) Asymmetry of chimpanzee planum temporale: Humanlike pattern of Wernicke's brain language area homolog. *Science* 279, 220–222
- Moffat, S.D. *et al.* (1998) Morphology of the planum temporale and corpus callosum in left handers with evidence of left and right hemisphere speech representation. *Brain* 121, 2369–2379
- Hutsler, J. and Galuske, R.A.W. (2003) Hemispheric asymmetries in cerebral cortical networks. *Trends Neurosci.* 26, 429–436
- Booth, J.R. *et al.* (2003) Relation between brain activation and lexical performance. *Hum. Brain Mapp.* 19, 155–169
- Sharp, D.J. *et al.* (2004) Retrieving meaning after temporal lobe infarction: The role of the basal language area. *Ann. Neurol.* 56, 836–846
- Coulson, S. and Williams, R.F. (2005) Hemispheric differences and joke comprehension. *Neuropsychologia* 43, 128–141
- Chiarello, C. *et al.* (2003) Priming of strong semantic relations in the left and right visual fields: a time course investigation. *Neuropsychologia* 41, 721–732
- Faust, M. and Lavidor, M. (2003) Semantically convergent and semantically divergent priming in the cerebral hemispheres: lexical decision and semantic judgment. *Brain Res. Cogn. Brain Res.* 17, 585–597
- Taylor, K.I. *et al.* (1999) Qualitative hemispheric differences in semantic category matching. *Brain Lang.* 70, 119–131
- Titone, D. (1998) Hemispheric differences in context sensitivity during lexical ambiguity resolution. *Brain Lang.* 65, 361–394
- Federmeier, K.D. and Kutas, M. (1999) Right words and left words: Electrophysiological evidence for hemispheric differences in meaning processing. *Brain Res. Cogn. Brain Res.* 8, 373–392
- Grose-Fifer, J. and Deacon, D. (2004) Priming by natural category membership in the left and right cerebral hemispheres. *Neuropsychologia* 42, 1948–1960
- Kiefer, M. *et al.* (1998) Right hemisphere activation during indirect semantic priming: Evidence from event-related potentials. *Brain Lang.* 64, 377–408
- Abdullaev, Y.G. and Posner, M.I. (1997) Time course of activating brain areas in generating verbal associations. *Psychol. Sci.* 8, 56–59
- Beeman, M. *et al.* (1994) Summation priming and coarse coding in the right hemisphere. *J. Cogn. Neurosci.* 6, 26–45
- Maguire, E.A. *et al.* (1999) The functional neuroanatomy of comprehension and memory: The importance of prior knowledge. *Brain* 122, 1839–1850
- Mazoyer, B.M. *et al.* (1993) The cortical representation of speech. *J. Cogn. Neurosci.* 5, 467–479
- Stowe, L.A. *et al.* (1999) Sentence comprehension and word repetition: A positron emission tomography investigation. *Psychophysiology* 36, 786–801
- Beeman, M.J. *et al.* (2000) Right and left hemisphere cooperation for drawing predictive and coherence inferences during normal story comprehension. *Brain Lang.* 71, 310–336
- Brownell, H.H. *et al.* (1986) Inference deficits in right brain-damaged patients. *Brain Lang.* 27, 310–321
- Beeman, M. (1993) Semantic processing in the right hemisphere may contribute to drawing inferences during comprehension. *Brain Lang.* 44, 80–120

- 44 Ferstl, E.C. and von Cramon, D.Y. (2001) The role of coherence and cohesion in text comprehension: An event-related fMRI study. *Brain Res. Cogn. Brain Res.* 11, 325–340
- 45 Brownell, H.H. *et al.* (1990) Appreciation of metaphoric alternative word meanings by left and right brain-damaged patients. *Neuropsychologia* 28, 375–383
- 46 Anaki, D. *et al.* (1998) Cerebral hemispheric asymmetries in processing lexical metaphors. *Neuropsychologia* 36, 353–362
- 47 Schmidt, G.L. *et al.* Right hemisphere metaphor processing? Characterizing the lateralization of semantic processes. *Brain Lang.* (in press)
- 48 Rapp, A.M. *et al.* (2004) Neural correlates of metaphor processing. *Brain Res. Cogn. Brain Res.* 20, 395–402
- 49 Bowden, E.M. *et al.* (2005) New approaches to demystifying insight. *Trends Cogn. Sci.* 9, 322–328
- 50 Fiore, S. and Schooler, J. (1998) Right hemisphere contributions to creative problem solving: Converging evidence for divergent thinking. In *Right Hemisphere Language Comprehension: Perspectives from Cognitive Neuroscience* (Beeman, M. and Chiarello, C., eds), pp. 255–284, Erlbaum
- 51 Jung-Beeman, M. *et al.* (2004) Neural activity when people solve verbal problems with insight. *PLoS Biol.* 2, E97
- 52 Ellison, A. *et al.* (2004) An exploration of the role of the superior temporal gyrus in visual search and spatial perception using TMS. *Brain* 127, 2307–2315
- 53 Barch *et al.* (2000) Anterior cingulate and the monitoring of response conflict: Evidence from an fMRI study of overt verb generation. *J. Cogn. Neurosci.* 12, 298–309
- 54 Kan, I.P. and Thompson-Schill, S.L. (2004) Selection from perceptual and conceptual representations. *Cogn. Affect. Behav. Neurosci.* 4, 466–482
- 55 Miller, E.K. and Cohen, J.D. (2001) An integrative theory of prefrontal cortex function. *Annu. Rev. Neurosci.* 24, 167–202
- 56 Rowe, J.B. *et al.* (2000) The prefrontal cortex: response selection or maintenance within working memory? *Science* 288, 1656–1660
- 57 Thompson-Schill, S.L. *et al.* (1997) Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A re-evaluation. *Proc. Natl. Acad. Sci. U. S. A.* 94, 14792–14797
- 58 Zhang, J.X. *et al.* (2004) Is left inferior frontal gyrus a general mechanism for selection? *Neuroimage* 23, 596–603
- 59 Wagner, A.D. *et al.* (2001) Recovering meaning: Left prefrontal cortex guides controlled semantic retrieval. *Neuron* 31, 329–338
- 60 Milham, M.P. *et al.* (2001) The relative involvement of anterior cingulate and prefrontal cortex in attentional control depends on nature of conflict. *Brain Res. Cogn. Brain Res.* 12, 467–473
- 61 Robertson, D.A. *et al.* (2000) Functional neuroanatomy of the cognitive process of mapping during discourse comprehension. *Psychol. Sci.* 11, 255–260
- 62 Seger, C.A. *et al.* (2000) fMRI evidence for right hemisphere involvement in processing unusual semantic relationships. *Neuropsychology* 14, 361–369
- 63 Rogers, T.T. and McClelland, J.L. (2004) *Semantic Cognition: A Parallel Distributed Processing Approach*, MIT Press
- 64 Tardif, E. and Clarke, S. (2001) Intrinsic connectivity of human auditory areas: a tracing study with Dil. *Eur. J. Neurosci.* 13, 1045–1050
- 65 Galuske, R.A.W. *et al.* (2000) Interhemispheric asymmetries of the modular structure in human temporal cortex. *Science* 289, 1946–1949
- 66 Beauchamp, M.S. *et al.* (2004) Unraveling multisensory integration: patchy organization within human STS multisensory cortex. *Nat. Neurosci.* 7, 1190–1192
- 67 Behrmann, M. and Kimchi, R. (2003) What does visual agnosia tell us about perceptual organization and its relationship to object perception? *J. Exp. Psychol. Hum. Percept. Perform.* 29, 19–42
- 68 Hutsler, J. and Galuske, R.A.W. (2003) Hemispheric asymmetries in cerebral cortical networks. *Trends Neurosci.* 26, 429–435

Endeavour

the quarterly magazine for the history and philosophy of science

You can access *Endeavour* online via *ScienceDirect*, where you'll find a collection of beautifully illustrated articles on the history of science, book reviews and editorial comment.

featuring

Selling the silver: country house libraries and the history of science by Roger Gaskell and Patricia Fara

Carl Schmidt – a chemical tourist in Victorian Britain by R. Stefan Ross

The rise, fall and resurrection of group selection by M.E. Borello

Mary Anning: the fossilist as exegete by T.W. Goodhue

Caroline Herschel: 'the unquiet heart' by M. Hoskin

Science in the 19th-century zoo by Oliver Hochadel

The melancholy of anatomy by P. Fara

and coming soon

Etienne Geoffroy St-Hillaire, Napoleon's Egyptian campaign and a theory of everything by P. Humphries

Losing it in New Guinea: The voyage of HMS *Rattlesnake* by J. Goodman

The accidental conservationist by M.A. Andrei

Powering the porter brewery by J. Sumner

Female scientists in films by B.A. Jones

and much, much more . . .

Locate *Endeavour* on *ScienceDirect* (<http://www.sciencedirect.com>)