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What's 'Right' in Language Comprehension: Event-Related Potentials Reveal Right Hemisphere Language Capabilities

Kara D. Federmeier,* Edward W. Wlotko and Aaron M. Meyer
University of Illinois, Urbana-Champaign

Abstract

Although the term 'nonverbal' is often applied to the right cerebral hemisphere (RH), a growing body of work indicates that the RH can comprehend language and, indeed, that it makes critical contributions to normal language functions. Reviewed here are studies that have examined RH language capabilities by combining visual half-field presentation methods with event-related potential (ERP) measures. Because they afford temporal and functional specificity and can be obtained as participants simply process language for meaning, ERPs provide especially valuable insights into RH language functions. Such studies suggest that the RH appreciates word- and message-level meaning information, and that it may play a particularly important role in the processing of relatively unpredictable semantic relationships. In addition, this work suggests that patterns observed for everyday language processing may often be an emergent property of multiple, distinct mechanisms operating in parallel as the left and right hemispheres jointly comprehend language.

In some respects, modern cognitive neuroscience can trace its origins to studies of hemispheric asymmetries, as Paul Broca's demonstration (1861) of a link between speech and the left frontal operculum provided the first widely accepted evidence for cerebral specialization. In fact, language remains perhaps the most well-known of the many asymmetries that have now been documented, which range from differences in the processing of basic sensory features to biases in attention, emotional processing, and many aspects of higher cognition (e.g., Hellige 1993). It is well-known that damage to left hemisphere areas, especially in the inferior frontal cortex and insula and the superior temporal gyrus, can result in profound and sometimes permanent language deficits (aphasia). In contrast, similar damage to the right hemisphere is not generally associated with such notable language problems. Indeed, because of this striking dissociation, the left hemisphere (LH) is often referred to as the 'verbal' hemisphere and the right hemisphere (RH) as the 'nonverbal' hemisphere.

However, as early as 1874, John Hughlings Jackson suggested that this global categorization of the hemispheres was oversimplified. He hypothesized instead that 'the right hemisphere is the one for the most automatic use of words, and the left the one in which automatic use of words merges into voluntary use of words – into speech' (Jackson 1915 reprint). In particular, Jackson believed that, in contrast to language production, language comprehension is a bilateral function. Research since that time seems to have proven Jackson right. Work with patients undergoing language assessments prior to surgery (e.g., using the intracarotid amobarbital procedure to temporarily anesthetize each of the hemispheres) has suggested that it is rare for the RH to be able to control speech (e.g., Risse et al. 1997). However, studies of commissurotomized patients, individuals who have had the connections between their hemispheres severed in order to control medically intractable epilepsy, suggest that the isolated RH does seem to be able to understand both auditory and visual language, including abstract and concrete nouns, verbs, adjectives, and some function words, and to appreciate a variety of semantic relationships (Baynes and Eliassen 1998). It is perhaps not surprising, therefore, that studies using hemodynamic measures [i.e., positron emission tomography (PET) or functional magnetic resonance imaging (fMRI), which track blood flow or blood oxygenation levels to examine the localization of function in the intact brain] have often reported activity in both cerebral hemispheres during language comprehension (for reviews, see Bookheimer 2002; Gernsbacher and Kaschak 2003). For example, Xu et al. (2005) examined brain responses to isolated words, individual sentences, and connected narratives and found that activation in many regions – including perisylvian, extrasylvian, and premotor cortical areas and the cerebellum – became increasingly bilateral as complexity increased.

Beyond demonstrating that the RH is capable of some degree of language comprehension, such findings emphasize that the full range of normal language functions may require processing resources that are distributed across the two cerebral hemispheres. Indeed, studies of patients with unilateral brain damage have pointed to a number of roles for the RH in comprehension, including processing discourse meaning and structure (Wapner et al. 1981; Delis et al. 1983; Gardner et al. 1983), drawing and revising inferences (Brownell et al. 1986; Beeman 1993), and appreciating various forms of nonliteral language (Brownell et al. 1983; Weylman et al. 1989). For instance, Klepousniotou and Baum (2005) found that patients with unilateral RH damage failed to show facilitation (priming) for targets related to the metaphorical meanings of prime words (e.g., *chicken-scared*), even when those words were embedded in sentence contexts that supported the metaphorical reading. In contrast, patients with LH damage and non-brain-damaged control participants did show such priming, suggesting that an intact RH is needed for normal processing of figurative word meanings. Whether the RH makes language-specific contributions to such functions or provides more general

processing resources is a topic of current debate (see, for example, Monetta et al. 2006).

The Visual Half-Field Technique and Event-Related Potentials

The role of the RH in language comprehension has also been examined in brain-intact participants through the use of the visual half-field (VF) presentation technique (for a review, including a discussion of the limitations of this technique, see Banich 2002). This technique makes use of the fact that information presented in the visual periphery (more than about half a degree of visual angle from fixation) is exclusively projected to primary visual cortex on the contralateral side. By the time processing reaches higher-order visual areas, there is the potential for information-sharing between the two hemispheres via the corpus callosum and other cerebral commissures. However, because intrahemisphere connections outnumber callosal fibers by a factor of at least a thousand, it seems clear that it is not possible for all information to be transferred (Bogen 1990). Furthermore, information that is transferred is subject to a delay on the order of at least 10–15 ms (Hoptman and Davidson 1994). Thus, the hemisphere that apprehends the stimulus directly has a processing advantage in terms of both information quality and time, and, as a result, VF methods can induce processing biases that reveal functional asymmetries in the intact brain. Trials in which the RH is stimulated via presentation to the left visual field are often referred to as lvf/RH trials, and those stimulating the LH via right visual field presentation are abbreviated as rvf/LH.

Much of the research using VF methods to examine language comprehension has employed traditional behavioral psycholinguistic measures such as naming or lexical decision (word/nonword judgment) times. However, more recently, several investigators have begun combining VF methods with measurements of brain electrical activity in the form of event-related potentials (ERPs). When neurons are aligned and active at about the same time, their summed electrical activity can be measured with electrodes placed on the scalp, creating the electroencephalogram (EEG). ERPs are small voltage fluctuations in the EEG that are correlated in time with sensory or motor events (for a review, see Fabiani et al. 2007). Studies of the relations between ERP measures, stimulus and task factors, and behavioral measures have identified components of the ERP as markers of specific cognitive operations. For example, the N400 component, a negative wave peaking around 400 ms after stimulus onset, has proven an especially useful measure of semantic processing (for a review, see Kutas and Federmeier 2001). All potentially meaningful items (including visual and auditory words, pictures, and environmental sounds) elicit this response, and the amplitude of the N400 shows a strong, inverse correlation with the predictability of the eliciting stimulus within a given list, sentence, or discourse context (e.g., Kutas and Hillyard 1984; Bentin et al. 1985). The N400, however, is generally

insensitive to grammatical violations and other manipulations that do not affect meaning (Kutas and Hillyard 1980, 1983). It is thus a sensitive and functionally specific measure of meaning access and integration.

A key advantage of ERP measures for the study of language asymmetries is that they can be collected while subjects simply read for comprehension, circumventing the difficulty of disentangling hemispheric differences in language processing from asymmetric competencies for specific tasks. Naming, for example, is known to be under LH control in most people, and studies of commissurotomized patients suggest that lexical decision judgments underestimate the semantic capabilities of the RH (Baynes and Eliassen 1998). Thus, ERPs provide an especially important window into the language capabilities of the RH.

Several other advantages of ERPs for the study of language asymmetries also deserve mention. Eye movements elicit electrical changes that can be picked up from electrodes placed near the eyes (the electro-oculogram or EOG). Because EOG is generally measured concurrently, the use of ERPs provides a natural means of ascertaining that participants maintain central fixation. This allows for the use of longer presentation durations than are typical in behavioral VF studies, a factor that is important because RH word apprehension seems less efficacious than LH word apprehension (Jordan et al. 2003) and is likely correspondingly more disadvantaged by very brief presentations of word stimuli. Second, because ERPs are a multidimensional measure – revealing not only the size but also the precise timing and (when multiple electrodes, spaced over the head, are used) the spatial distribution of effects – they provide a means for inferring the underlying nature of any VF-based differences that might occur (for a detailed discussion of inference-drawing from ERPs, see Rugg and Coles 1995). For example, if processing is mediated by callosal transfer (e.g., if a particular function can be performed only by the LH, such that with lvf presentation the information must first be transferred from the RH to the LH), then condition-related effects following rvf and lvf presentation should differ in latency but not in scalp distribution (as exactly the same brain areas are ultimately involved). In contrast, if RH and LH areas are active in parallel but to differing degrees depending on the VF-induced processing bias, then rvf and lvf presentation are likely to yield effects that begin at the same time but that differ in their distribution over the head (e.g., possibly larger over one hemisphere than the other).

Finally, and perhaps most importantly, ERPs allow for the simultaneous and specific assessment of asymmetries at multiple processing levels. It is thus possible to go beyond knowing simply that the hemispheres process information differently and to begin building an understanding of when and how such differences arise. One can thus ask whether, for instance, sensory-, attention-, semantic-, syntactic-, memory-, and/or response-related aspects of processing are asymmetric, and, if so, how these asymmetries relate to one another and to hemispheric biases evident in behavior. Because of these

methodological advantages,[1] studies combining VF presentation techniques with the concurrent measurement of ERPs have provided some important data about the nature of language asymmetries and the role of the RH in normal language comprehension, which are reviewed in the sections that follow.

Word Processing

A substantial body of literature using VF methods with behavioral measures has pointed to hemispheric differences in the breadth and/or timing of semantic activation. For example, studies using prime-target pairs lateralized to the rvf or lvf have indicated that words that are related solely on the basis of shared semantic features (as in distant category members, such as *dog-goat*) elicit facilitation early in processing in the rvf/LH, but become active more slowly and stay active longer in the lvf/RH (e.g., Koivisto 1997). In contrast, words that both share semantic features in common and are lexically associated (typically defined as the tendency for one word to elicit another in word generation tasks; e.g., *dog-cat*) show facilitation in both VFs both early and later in processing (Chiarello et al. 2003). Building on work like this, several studies have used ERPs and VF presentation methods to examine each hemisphere's ability to process various types of semantic relationships. A number of these studies have suggested a LH bias for the processing of lexically associated information but a RH bias for the processing of categorical information.

For example, Deacon et al. (2004) presented participants with prime-target pairs that were either associated but did not share semantic features (e.g., *dog-bone*) or that shared features but were not lexically associated. For the associated pairs, they observed significant N400 facilitation (reduced amplitudes for related, relative to unrelated, targets) with rvf/LH presentation but not with lvf/RH presentation, whereas for the similar pairs they observed N400 facilitation with lvf/RH but not rvf/LH presentation. In a follow-up study, Grose-Fifer and Deacon (2004) compared facilitation for categorically related word pairs with high (e.g., *mosquito-flea*) and low (e.g., *sofa-vase*) levels of feature overlap and determined that the RH's advantage for the processing of categorical pairs was due to shared features: N400 facilitation was observed only for the pairs with high overlap, and then only with lvf/RH presentation. Other studies using similar designs have also failed to find N400 priming for categorically related but unassociated word pairs in the rvf/LH (Bouaffre and Faita-Ainseba 2007), and patients with damage to the RH have been found to lack a categorical priming effect on the N400 (Hagoort et al. 1996). Thus, the RH seems to play an important role in linking words that share features but are not highly expected to occur together. The tendency for associative information to be more readily processed in the rvf/LH has also been replicated, though the exact pattern of results has been more variable across studies. Some studies found no effect of lexical association

for lvf/RH presentation (Atchley and Kwasny 2003, which looked at the processing of words associated with the dominant and subordinate meanings of homographs), some found a delayed effect (Bouaffre and Faita-Ainseba 2007, who observed no N400 facilitation for lexical associates presented in the lvf/RH but did observe priming effects in a later time window, on the late positive complex, which has been linked to more explicit aspects of semantic processing), and some found N400 facilitation that was smaller in magnitude than that observed for rvf/LH presentation (Coulson et al. 2005).

A number of explanations have been put forward for this pattern of asymmetries. Some researchers (e.g., Bouaffre and Faita-Ainseba 2007) have linked these results to the 'coarse coding hypothesis', which suggests that semantic activation is focal and strong in the LH but broader and weaker in the RH (Beeman 1998; Jung-Beeman 2005). On this account, the categorical priming advantage for the RH arises because unassociated category members tend to be weakly related. In contrast, Deacon and her colleagues (2004) have suggested that such asymmetries arise because the hemispheres employ fundamentally different kinds of semantic representation. They argue that LH semantic processing is holistic, utilizing localist representations connected via associative links, which can be primed through spreading activation. In contrast, they posit that the RH uses distributed, feature-based representations, such that priming occurs due to the overlap in activation engendered when two words with similar features are processed in close temporal proximity. A third possible explanation is suggested when the patterns of word pair priming are integrated with results seen in studies of sentence processing (described next). In particular, sentence processing studies point to differences in how the two hemispheres make use of context information, with the LH biased toward processing words in an anticipatory, 'predictive' fashion and the RH biased toward processing in a more post hoc, 'integrative' fashion (see review in Federmeier 2007). Because lexical association is defined on the basis of predictability (i.e., targets are defined as lexically associated with their primes if the prime words lead people to expect, and thus generate, the targets), this type of relationship might be especially well-suited to LH processing strategies. In contrast, unassociated categorical relationships are typically quite unpredictable – but their relationship can often readily be appreciated post hoc. Irrespective of the particular mechanism involved, however, all three accounts converge in suggesting a special role for the RH in the processing of less well-established word relations.

Sentence Processing

While contributing to our understanding of single word processing, ERPs have thus far had their greatest impact in elucidating the RH's ability and tendency to make use of the richer context information afforded by sentences and other higher level language structures. Behavioral work examining

hemispheric asymmetries in sentence processing has yielded mixed results, with a number of studies suggesting that the RH is incapable of deriving the message-level meaning of a sentence (see, for example, review in Faust 1998), but a few, more recent studies suggesting at least a limited capability to appreciate message-level coherence (Chiarello et al. 2001; Faust et al. 2003). For example, one study examined hemispheric sensitivity to word-level and message-level information by comparing lexical decisions to sentence-final target words preceded by associated or nonassociated primes embedded in several types of contexts (Faust et al. 2003). Both hemispheres showed facilitation for associated targets in congruent contexts but inhibition for these same words when embedded in incongruent contexts, suggesting a basic sensitivity on the part of the RH to the message-level fit of the words. However, these effects were larger for the rvf/LH, leading the authors to conclude that the LH is the primary substrate for message-level computations, with the RH biased instead toward the processing of word-level relationships. In contrast, ERP data have consistently shown that the RH can and does make use of message-level context information, albeit in a manner that differs from the LH.

The first ERP evidence that the RH has access to message-level representations came from a study using lateralized words that completed sentences as the most expected ending or as an anomalous ending that was or was not categorically related to the most expected ending [e.g., 'They wanted to make the hotel look more like a tropical resort. So along the driveway they planted rows of palms/pines/tulips.' (Federmeier and Kutas 1999a)]. Both hemispheres showed a clear sensitivity to sentence-level congruity, with smaller N400s to expected than to unexpected between-category words; the magnitude of this effect was, in fact, identical across the two VFs. Differences between the hemispheres emerged, however, in the response to unexpected words that came from the same semantic category as the expected completions (e.g., *pines*), as these showed N400 facilitation relative to the between-category violations only with rvf/LH presentation. Note that, in contrast to the results from studies examining word-pair priming, this pattern suggests that the LH can appreciate categorical relationships (the within category violations and expected completions shared features but were not lexically associated), but that it does so under different circumstances than the RH. In particular, whereas the RH seems to appreciate featural similarity between two words presented in close succession, the LH seems sensitive to feature overlap between a word that is presented and another that was expected (but never actually presented) in the context. The pattern seen for rvf/LH presentation is identical to that seen with central presentation (Federmeier and Kutas 1999b), and has been associated with the predictive use of context information, in which features of likely upcoming words are preactivated as context accrues (see review in Federmeier 2007). In contrast, processing in the lvf/RH seems to be more driven by the plausibility of a given ending in its context. Federmeier and Kutas (1999a)

termed this an 'integrative' processing style (similar to that posited in many extant theories of language comprehension), in which each word is processed in a fairly stimulus-driven fashion and then fit into the context in a more post hoc manner. The asymmetric N400 pattern was replicated when the sentence frames were completed with lateralized pictures rather than lateralized words (Federmeier and Kutas 2002), showing that it indexes something general about how each hemisphere integrates semantic information with context, as opposed to something particular about word-reading.

The data from Federmeier and Kutas (1999a) suggest that the RH has the ability to appreciate the fit of individual words to a larger-scale context. However, some have suggested that although the RH can (at least sometimes) appreciate message-level congruity, it is biased to process word-level over message-level relationships when both information sources are available (e.g., Faust et al. 2003). To examine this possibility, Coulson et al. (2005) pitted message-level information against word-level information by using lateralized congruous or incongruous completions that either were or were not associated with a word in the prior sentence context. An example of a sentence pair with (1), an unassociated congruous and an associated incongruous ending, and (2), an associated congruous and unassociated incongruous ending, is:

(1) 'They were hard to walk in, but she loved her olive shoes/oil.'
(2) 'The Italian cook always added too much olive oil/shoes.'

As already described, when lateralized words (*oil*) were primed by associates (*olive*) outside of context, N400 responses were facilitated in both VFs, with a slightly larger effect for rvf/LH presentation. When these word pairs were embedded in sentence contexts, both hemispheres evidenced strong N400 congruity effects (smaller responses to congruous as compared with anomalous words), which were statistically indistinguishable. However, in striking contrast to Faust et al.'s (2003) predictions, these effects of message-level congruity largely swamped word association effects in both hemispheres. In the sentence contexts, responses to associated words were only slightly more positive than those to unassociated words. With rvf/LH presentation, these small association effects were evident only for incongruous sentence completions, whereas they were present for both incongruous and congruous completions after lvf/RH presentation. These results suggest that both hemispheres primarily rely on message-level information when it is available. That the RH but not the LH showed some associative priming within congruous sentences might suggest that the RH is more sensitive to word–word relationships in higher level contexts than is the LH. However, the RH does not seem to rely on word-level information to a greater extent than it relies on message-level information.

Thus far, the ERP data make clear that the RH's appreciation of message-level congruity is on par with that of the LH. However, it is possible that basic congruity can be inferred via an assessment of the global fit between the

critical word and other words in the sentence, without the need to truly construct a coherent message-level representation. As a stronger test of the RH's ability to make use of sentence-level information, Federmeier, Mai and Kutas (2005) compared the response to strongly constrained and weakly constrained (but plausible) sentence endings. Critical words had no strong lexical association with any of the words in the sentence context, and, because all endings were plausible, word-level relationships alone would not provide much power to distinguish the strongly from the weakly constrained completions. Nevertheless, strongly constrained endings elicited smaller N400s than weakly constrained endings in both VFs, and the constraint effect was indistinguishable in size and timing across VF, except for interactions with topographic variables suggesting that the scalp distribution of the N400 was skewed contralateral to VF of presentation (an indication that the VF technique successfully biased processing toward the hemisphere that initially apprehended the stimulus). Thus, there was again no evidence that the RH was less able or likely than the LH to make use of higher level context information to shape its word processing. Indeed, across studies, the similarity across VF in the size and timing of basic sentence-level N400 effects such as congruency and constraint is quite striking, given that response times and accuracy are usually strongly skewed in favor of the rvf/LH (a factor that renders interpretation of asymmetries more difficult for these measures). Thus, these ERP studies suggest that the two hemispheres share similar capabilities to make use of message-level meaning information that is not solely based on word-level relationships, although that information does not seem to impact processing in precisely the same ways in the RH as in the LH.

An understanding of asymmetries in other aspects of message-level processing awaits further investigation. For example, several ERP studies using patients with unilateral brain damage suggest that the LH may construct message-level representations more quickly than the RH (e.g., Swaab et al. 1997, 1998) or that the LH and RH may weight syntactic and semantic information differently (e.g., Hagoort et al. 2003; see also ter Keurs et al. 1999; Wassenaar et al. 2004; Wassenaar and Hagoort 2005). How findings at the sentence level extend to larger discourses and texts is also a question that still awaits investigation with these methods. ERPs can provide an especially useful window into the processing of larger language structures, as they are a continuous measure that can be examined at multiple points in the processing stream – thus, allowing insight into how meaning information accrues and is revised over time.

The construction of message-level information may also differentially affect processing at the perceptual level. For example, although in the Federmeier et al. (2005) study, semantic processing was similarly affected by constraint in the two VFs, differences between the hemispheres did emerge at other processing levels, as the frontal P2 was modulated by sentential constraint only with rvf/LH presentation. Thought to be an index of higher level visual processing, the P2 effect was interpreted by Federmeier et al. (2005)

as reflecting facilitated visual processing for strongly constrained endings as a result of top-down, predictive preactivation of likely upcoming words. Because this effect was only observed for rvf/LH presentation, this interpretation fits with the proposal that the LH engages in predictive processing, whereas the RH adopts a more 'wait-and-see' approach (see also Federmeier and Kutas 2002; Evans and Federmeier 2007; Wlotko and Federmeier 2007 for other VF-based P2 differences).

The kind of prediction-based comprehension strategy postulated for the LH would seem to afford a processing advantage under many circumstances, as the use of context information to prepare for the processing of likely upcoming words can be efficient and robust under many conditions (see Federmeier 2007 for a more extensive discussion of the role of prediction in language comprehension). However, such a strategy can also fail, either when context information is weak or when expectations are violated. Indeed, it is for these very reasons that many language-comprehension frameworks have eschewed prediction. If a predictive system is supplemented by a more stimulus-driven processing strategy of the type suggested for the RH, however, then the combined system would seem especially well-suited to solve the problems associated with comprehending the rapid, structured – but sometimes unpredictable – information contained in speech or written text. Evidence that normal comprehension indeed reflects a blend of the two hemispheres' processing styles was obtained in a study (Wlotko and Federmeier 2007) that jointly manipulated expectancy and sentential constraint. A well-replicated finding in the ERP language literature is that N400 amplitudes are graded by cloze probability (i.e., in offline tasks, the percentage of people who choose to complete a given sentence frame with a particular word; Taylor 1953). Thus, the response to a word with low to moderate cloze probability is generally intermediate between the response to a high cloze probability completion and that to an unexpected completion, with a cloze probability near zero (e.g., Kutas and Hillyard 1984). Strikingly, Wlotko and Federmeier (2007) found that neither hemisphere individually showed the graded N400 pattern; instead, responses to completions of moderate cloze probability (here, expected endings of weakly constraining contexts) were highly facilitated with rvf/LH presentation (similar in amplitude to the response to high cloze probability completions of strongly constraining contexts), but were not facilitated relative to unexpected completions with lvf/RH presentation. When the responses of the two hemispheres were averaged together, however, the expected, graded N400 amplitude pattern (seen for these same stimuli with central presentation; Federmeier et al. 2007) emerged. Findings like these emphasize that patterns of results seen for normal language processing may often reflect critical contributions from RH processing strategies and thus highlight the importance of understanding the RH's language-processing capabilities for building a complete picture of the mechanisms involved in comprehension.

Nonliteral Language Processing

Some of the earliest evidence that the RH plays a role in normal language comprehension came from the domain of nonliteral language processing. Work with RH-damaged patients has uncovered processing deficits for a variety of types of nonliteral language, including idioms (Van Lancker and Kempler 1987), jokes (Brownell et al. 1983), and metaphors (Winner and Gardner 1977). Notably, the processing of such language structures requires not only a basic understanding of words and sentences, but also the ability to recruit appropriate background knowledge and apply it to or contrast it with the message-level meaning of the language context.

For example, appreciating a typical one-line joke (e.g., 'When I asked the bartender for something cold and full of rum, he recommended his wife.') involves noting the surprising element (*wife* instead of *daiquiri*), accessing new knowledge to allow the reinterpretation of specific prior elements in the context (e.g., *cold* = *unemotional*), and revising the message-level meaning correspondingly. Early research that investigated the ability of RH-damaged patients to understand jokes pointed to a particular difficulty with the 'coherence' aspect of joke comprehension, rather than the 'surprise' aspect (Brownell et al. 1983), suggesting that the RH's role involved the meaning construction process itself, and not just the emotional aspect of joke processing. To examine how the two hemispheres use language context information and background knowledge in tandem in order to construct meaning, Coulson and Williams (2005) recorded ERPs to sentences with laterally presented expected endings (*daiquiri*), joke endings (*wife*), or similarly unexpected but straightforward sentence completions (e.g., *mojito*). With central presentation, unexpected straight endings elicited smaller N400 responses than joke endings (Coulson and Kutas 2001), and this pattern was replicated in the rvf/LH. However, for lvf/RH presentation, jokes were facilitated to the same degree as straight completions, suggesting that the RH's use of context information afforded it an advantage for integrating the joke-related meaning. A follow-up study by Coulson and Wu (2005) used the same kind of stimuli but examined the response to lateralized probe words that followed the (centrally presented) joke and nonjoke sentence endings. They reported more N400 facilitation for probes related to joke endings (e.g., *frigid*, following the bartender joke above) when these were presented in the lvf/RH, which is consistent with the idea that the RH activates more joke-related information than the LH.

The RH's tendency to show facilitation for a broader range of completions than the LH in these studies might be seen as arising from less 'precision' in its semantic processing (i.e., coarse coding). However, results of studies looking at other types of nonliteral language argue against the idea that RH activation is always broader than LH activation. For example, a study by Coulson and Severens (2007) investigated each hemisphere's ability to

appreciate puns, such as 'During branding, cowboys have sore calves.' Whereas appreciating a joke requires a switch from one interpretation of the discourse message to another, appreciating a pun requires the active maintenance of multiple, contextually appropriate meanings of an ambiguous word or phrase. Coulson and Severens (2007) recorded ERPs to laterally presented probe words (e.g., *cows* or *legs*) following an auditorily presented pun. When the probes immediately followed the pun, facilitation was seen in the rvf/LH for words associated with both of the pun word's meanings, but facilitation in the lvf/RH was limited to the most prominent meaning. After a delay of 500 ms, activation for both meanings was seen in both hemispheres. Thus, counter to the predictions of coarse coding, in this case the RH did not show a greater tendency to activate meaning information more broadly; instead, its activation of the more weakly related information was actually delayed relative to the LH. Similarly, a study of metaphor processing (Coulson and Van Petten 2007) found no differences in the ability of the LH and RH to appreciate metaphorical meanings of words in sentences.

Thus, parallel in some ways to the conclusions that have been drawn from word-pair priming studies, the work of Coulson and her colleagues suggests an important role for the RH in processing the relatively more novel semantic relations that arise in some, but not all, forms of nonliteral language. Both hemispheres seem to be able to process higher order language structures that involve the activation of multiple meanings associated with a particular word, including metaphorical senses. However, in cases where an initial semantic construal must be revised, the RH seems to outperform the LH. It is possible that this difference arises because the LH, in making predictions, is more likely than the RH to commit to a particular interpretative structure. Another, intriguing, possibility is that some asymmetries in high-level language processing may arise in part because of differences in the hemispheres' verbal memory abilities. In particular, the RH seems to be better at retaining specific information about words that it has encountered over long delays (Evans and Federmeier 2007). This capability may be particularly important for language processes that involve keeping track of and mapping between discourse referents over time or that require the reinterpretation of specific context words (as may often be the case when comprehending jokes).

Conclusions

In sum, since Paul Broca's initial discovery of asymmetric language processing, a large body of literature has been brought to bear on the question of how this most human of all cognitive processes is instantiated in the brain. Although the critical role of the LH in supporting key language functions is incontrovertible, John Hughlings Jackson's contention that the RH is also involved in normal language comprehension has now received extensive

empirical support, with particularly strong contributions from studies that have taken advantage of the strengths of ERP methods to examine RH language capabilities. Such studies suggest that the two hemispheres both have access to word- and message-level meaning information, but that they use this information in different ways. Indeed, it seems that the brain may be able to most efficaciously confront the difficulties inherent in dealing with a complex, rapid stream of information by implementing multiple processing strategies in parallel – e.g., across the hemispheres, by processing meaning both focally and broadly, rapidly and slowly, predictively and in a more stimulus-driven fashion, etc. However the specifics of these asymmetries may fall into place, it is clear that the full range of normal language-processing abilities requires the intact functioning of both cerebral hemispheres. As such, it is appropriate that our knowledge of RH comprehension abilities has expanded from the substantial literature on semantic processing at the word level to sentence- and discourse-level processes. Developing a complete understanding of how the brain maps between input and meaning requires that we continue to unravel the independent and interactive language-processing mechanisms of the two cerebral hemispheres.

Thus, an understanding of processing asymmetries continues to be important, even though, in the current era, it can be tempting to view studies of hemispheric specialization as 'quaint' – after all, designating a function as right or left may seem crude in the wake of research mapping specific cognitive processes onto increasingly more restricted subparts of brain structures. However, hemispheric specialization throws out a challenge to many explicit and implicit assumptions of modern cognitive neuroscience. The two hemispheres are overwhelmingly the same along most of the dimensions that are typically invoked when trying to understand brain–behavior relationships. LH brain areas associated with language, for example, have similar inputs and outputs and similar cell and neurotransmitter types to homologous areas of the RH. Yet, the hemispheres have strikingly different functional capabilities and biases. Thus, fairly subtle anatomical and physiological differences, of the type generally not yet even cataloged for most areas of the brain, must have large consequences for cognitive function; this is something that cognitive neuroscience will thus eventually need to come to terms with. Furthermore, cognitive and neurobiological frameworks that seek 'the' mechanism or 'the' brain area responsible for a particular behavior will need to consider the possibility that multiple mechanisms, perhaps distributed across the two cerebral hemispheres, may often be involved in a given function, and that the contributions of each may vary as a function of stimulus and task properties and the tendencies of individual subjects. Thus, far from being outmoded, studies of hemispheric differences – and of interhemispheric cooperation – promise to continue to offer probing questions and provide cutting-edge answers for studies of brain–behavior relations.

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Short Biography

Kara Federmeier obtained her PhD in Cognitive Science from the University of California, San Diego. She is currently an Assistant Professor in the Department of Psychology at the University of Illinois, Urbana-Champaign and the director of the Cognition and Brain Lab, housed at the Beckman Institute for Advanced Science and Technology. Her research, including recent papers in *Psychological Science*, the *Journal of Cognitive Neuroscience*, *Brain Research*, and *Neuropsychologia*, uses ERPs to examine brain mechanisms of meaning access and integration, including hemispheric differences in language comprehension, changes in language processing associated with normal aging, and the interplay of language and memory. A paper based on her address upon receiving the Society for Psychophysiology's Award for Distinguished Early Career Contributions to Psychophysiology was recently published in *Psychophysiology*.

Edward W. Wlotko's research focuses on understanding the use of context information as language comprehension unfolds, with an emphasis on hemispheric asymmetries in the use of sentential context. He holds a BS from the University of Pittsburgh and an MA from the University of Illinois at Urbana-Champaign.

Aaron Meyer received his PhD from the University of Missouri-Columbia. He is currently a postdoctoral researcher at the University of Illinois. His recent work has focused on word meaning selection in the cerebral hemispheres as revealed by eye tracking and ERPs, including the effects of aging on selection processes.

Notes

⋆ Correspondence address: Kara D. Federmeier, Department of Psychology, University of Illinois, Urbana-Champaign, 603 E. Daniel St, Urbana, IL 61820, USA. Email: kfederme@uiuc.edu.

[1] One disadvantage of ERP measures relative to behavioral ones is that more trials are typically required in ERP research, in order to obtain stable signals in individual participants.

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