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DISCOURSE AND THE BRAIN

Capturing meaning in the wild

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Introduction

Husband: “Hey, how was your day at work?”

Wife: “It felt so long. I had to speak with five different clients, and one of them is that stubborn one I’ve complained about before. The only break I had was when I walked to lunch with Susan; it was such a nice day out. When I get home, I just want to sit on the couch, eat some ice cream, and watch TV. How was yours?”

This semifictional phone conversation between a husband and his wife is just one example of “language in the wild,” or natural language. It begins with a question prompt, to which the wife responds by telling the story of her day. The husband, as an active listener, must then process the arbitrary speech signs and symbols produced by his wife, convert them to meaningful messages, and understand them within larger contexts such as prior knowledge (e.g., the “stubborn client” she had complained about before) and future plans (e.g., relax and watch TV). In interpreting linguistic and nonlinguistic signs, the husband and wife are semioticians, like the rest of us.

Understanding how the brain derives meaning from language’s arbitrary symbolic structure is foundational to neurosemiotics. The brain must not only extract meaning from isolated signs and symbols (e.g., individual sounds/words), but it must also interpret their meanings in the context of the information around them. The meaning of signs depends not just on the sign, but also on what is going on around the sign. A “thumbs up” sign means “everything is ok” or “I am with you” in many cultures. In scuba diving, though, it means “end the dive and rise to the surface.” This is also the case with linguistic signs such as words. If the wife in the above example is a doctor, then “client” refers to individuals with health problems. If the wife is a lawyer, then clients are individuals involved in legal disputes and nothing is implied about their health status. This surrounding information that helps construct meaning takes many forms, including prior words in a sentence and discourse, the tone of the speaker (likely exasperated in the given example), nonverbal gestures, and knowledge that has been communicated to us previously (Susan is a friend or coworker of the wife). How does the brain represent this information?

Over the past two decades, a rich body of research has examined the neural basis of representation of meaning expressed in language. Using neuroimaging, brain stimulation, and lesion methods, it has revealed a distributed set of regions forming a complex network that dynamically represents



various aspects of meanings of words and sentences (Binder & Desai, 2011; Binder et al., 2009; Desai & Riccardi, 2021). Most studies have relied on carefully selected word-, phrase-, and sentence-level stimuli. This choice is motivated by the fact that words have many psycholinguistic properties that are partly correlated with each other. To disentangle and pinpoint brain bases of any particular variable of interest (e.g., high imageability), it is necessary to control for myriad other variables (e.g., frequency, number of phonemes, orthographic and phonological neighbors) and to minimize the complex influence of context. This approach has provided fundamental and novel insights into how concepts are represented and processed in the brain, with wide-ranging theoretical and clinical implications (e.g., Lambon-Ralph et al., 2017). However, language in the wild does not often consist of single words or sentences that are not part of a larger discourse or narrative, defined here as language that is above sentence level. Naturalistic language takes multiple forms, many of which have distinct purposes. Narrative and expository genres are commonly distinguished (Clinton et al., 2020). Despite the variety, the main goal of virtually all natural language is to transfer information from one brain to another, a process sometimes referred to as “brain-to-brain coupling” (Hasson et al., 2012). To accomplish this coupling, multiple cognitive processes are required, including linking sentences together, integrating new information into the existing context, and learning relationships between concepts or characters within the discourse.

A growing body of research is aimed at examining not only how these discourse-level tasks are accomplished, but also the neural basis of lexical semantics and related psycholinguistic variables when language is processed in relatively naturalistic contexts (Kemmerer, 2021). This work is complementary to the traditional single-word and sentence-level approach and is essential to expanding our understanding of the representation of concepts in a more ecologically valid context, a topic of central importance to neurosemiotics. Here, we provide a brief overview of this research, focusing on fMRI studies – for a review of magnetoencephalographic and electroencephalographic studies, see Alday (2019). First, we discuss findings related to lexical semantics and related variables such as frequency and surprisal when words are processed in discourse context. Combinatorial operations and discourse-level processes are addressed next, followed by a discussion of the possible roles of major areas that are consistently implicated in discourse semantics. We conclude with cautions, caveats, and suggestions for future research.

Lexical processing in discourse context

Words have numerous psycholinguistic properties that have been studied using behavioral and neuroimaging methods. An interesting question is how or whether discourse context affects these variables. Here, we review some of the work that examines lexical variables in naturalistic context. Figure 11.1 shows activation peaks from several studies that parametrically examined some variables related to semantics (see also Table 11.1).

Word frequency

Different words are encountered at different rates in natural language. For example, the word “shop” happens much more often than the word “hippopotamus.” Word frequency refers to how often a given word occurs in language, measured by counting occurrences in large text and speech corpora. It is a central psycholinguistic variable that has salient effects in both comprehension and production, and it explains the most variance in standard psycholinguistic tasks, such as lexical decision, picture naming, and word naming (Adelman et al., 2014; Balota et al., 2004; Benkí, 2003). Neuroimaging research using single-word stimuli has found that low frequency words are typically associated with greater activity than high frequency words in areas such as the inferior frontal gyrus (IFG), the anterior insula, the intraparietal sulcus (IPS), and the visual wordform area (VWFA), with this activity

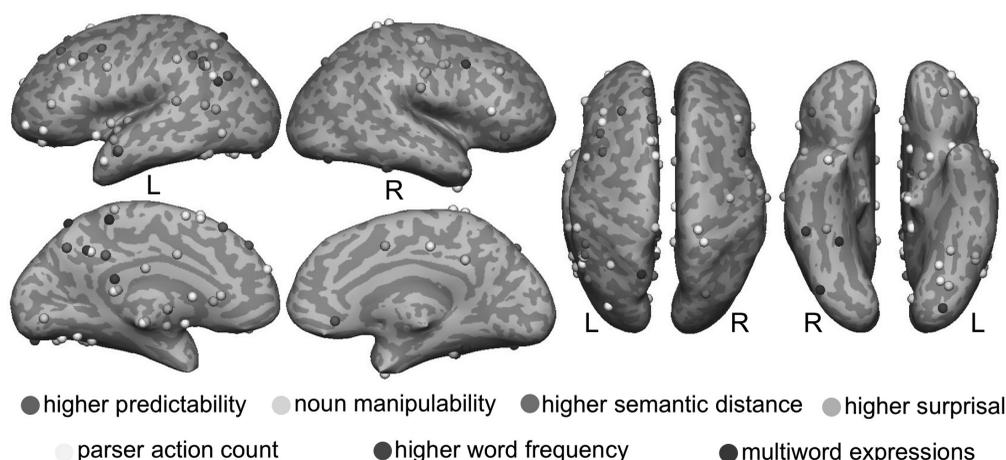


Figure 11.1 Activation peaks for several lexical variables studied in a discourse context
 Taken from Bhattasali et al. (2018), Desai et al. (2018), Frank and Willems (2017), Willems et al. (2016), and Desai et al. (2016). See e-book for a full-color version of this figure.

Table 11.1 Variables associated with major regions implicated in naturalistic language studies. AG: angular gyrus; ATL: anterior temporal lobe; pCu/pCi: precuneus/posterior cingulate

Area	Predictability	Semantic distance	Parser action count	Word frequency	Surprisal	Multiword expressions
AG	Π	Π	Π	Π		
ATL		Π	Π		Π	
pCu/pCi		Π	Π	Π	Π	Π

often being attributed to higher phonological, orthographic, or executive demands (Graves et al., 2010; Hauk et al., 2008; Yarkoni et al., 2008). Effects of higher frequency are more controversial, with several studies finding no effects and a few studies finding increased activation in temporal and inferior parietal areas associated with semantics (e.g., Graves et al., 2010). Behavioral studies indicate that higher frequency words have richer semantic representations, measured by several variables such as the number of semantic neighbors, number of features, contextual diversity, and number of associates (Pexman et al., 2007; Reilly & Desai, 2017). Stronger automatic activation of this information may be expected for higher frequency words.

To investigate effects of frequency in naturalistic contexts, Desai et al. (2020) used concurrent fMRI and eye-tracking while participants silently read 22 paragraphs of text. Co-registration of fMRI signal and fixations from eye-tracking allowed extraction of word-specific responses. Rapid serial visual presentation is often used in studies with sentence and discourse stimuli, where presentation rate of words is controlled experimentally. Allowing participants to read entire paragraphs presented on the screen provides a more naturalistic scenario, as the participant controls fixation duration on each word, can re-fixate, or can skip words entirely, closely approximating natural reading. Frequency was modeled as a predictor, controlling for the psycholinguistic confounds of concreteness, number of letters and syllables, and lexical and syntactic surprisal. Higher frequency was correlated with greater activity in areas commonly associated with semantic processing, including the bilateral angular gyrus (AG), the precuneus/posterior cingulate (pCu/pCi), and the anterior temporal lobe (ATL). The authors interpreted these findings as an extensive and automatic activation of the semantic system due to high frequency words having greater semantic richness, a relationship enhanced by the semantic

depth of a naturalistic context. This suggests that in some single-word studies, task-specific factors (e.g., the need to make a word/nonword response in a lexical decision task) may partially suppress this spread of activation, resulting in weaker positive correlations with frequency.

More strongly differing from single-word studies, this research showed relatively low levels of negatively correlated activity. The commonly seen activation in the IFG was missing. Lower frequency was correlated with greater activity in the left IPS and posterior supramarginal gyrus (SMG), which the authors attributed to attentional and phonological demands, respectively. Additionally, negatively correlated activity was reduced and a large cluster in the medial superior frontal gyrus (SFG) was eliminated after controlling for lexical and syntactic surprisal, suggesting that predictive processes during naturalistic reading may lower the neural costs of encountering low-frequency words. Methodologically, this study demonstrated that by using simultaneous eye-tracking and fMRI, a high temporal resolution signal can be extracted that enables study of word-level variables during naturalistic, self-paced narrative reading. This study also illustrates one dimension along which well-established results from single-word studies may differ when words are considered within the context of a narrative.

The above evidence reveals some effects of frequency on processing of linguistic symbols, and its interaction with context. These findings align with the basic semiotic insight that signs' meanings can vary with context. Due to richer semantic content (including both associations and features), a more extensive set of neuroanatomical areas is recruited to represent frequent signs. Effects of frequency are enhanced with naturalistic context, as deeper neural representation of individual symbols leads to more efficient textual integration and richer situation models.

Surprisal and entropy

The brain is constantly predicting what it will encounter next (Bubic et al., 2010), a feature that plays an important role in natural language processing. Multiple types of information are used during discourse to predict upcoming words and aid comprehension, including knowledge about the structure of the language (e.g., English has a subject-verb-object structure) and about the world (e.g., associated concepts). In an fMRI study, Willems et al. (2016) examined two aspects of prediction, surprisal and entropy, while participants passively listened to novel excerpts and their reverse as a control condition. Briefly, surprisal is defined as the probability of the current word given the previously encountered words (e.g., a word with high surprisal deviates significantly from what was expected). Entropy is defined as the probability distribution of all *upcoming* words at a given timepoint during a sentence. High entropy indicates that many different words are possible (low predictability), while low entropy means relatively few words are likely (high predictability). The authors used a computational model to give each content word in the novel a surprisal and entropy rating to reveal the neural correlates of these measures, while controlling for word frequency. High surprisal was associated with greater activity in the left VWFA, the bilateral STG and ATL, and the right IFG. Considering that the VWFA is sensitive to word forms and the STG comprises the primary and secondary auditory cortices, the authors interpreted activity in these areas as being related to lower-level auditory or wordform predictions that must be updated when encountering a surprising word. The bilateral ATL activity may be due to lexical-semantic integration demands, which are likely to increase in the event of high surprisal.

Low entropy was associated with increased activity in the right IFG, the left middle frontal gyrus (MFG), and the left AG. The authors speculated that the AG, which has been implicated as a semantic "convergence zone" (Binder & Desai, 2011; Bonner et al., 2013), may be involved in predicting the semantic content of the upcoming word. The IFG and MFG, on the other hand, have been associated with top-down domain-general processing. Here, their sensitivity to highly predictable words perhaps reflects their involvement in priming word representations that engage widely distributed in other brain areas.

These studies demonstrate that the brain constantly uses previous signs and symbols to predict what is coming next. When a word has high surprisal, indicating an unsuccessful prediction, multiple areas are recruited to update and integrate that unexpected symbol into the larger context. When a word is easily predicted (e.g., low entropy), spreading activation can ignite relevant features of the word before it is encountered, enabling efficient integration into context.

Semantic features

A vast body of literature has been devoted to understanding how semantic content is represented in the brain. This research has shown that the semantic system is widely distributed neuroanatomically, and that some parts of that system are preferentially involved in the representation of specific semantic features, while others are sensitive to many features. Broadly, studies have shown that the set of brain regions activated during naturalistic discourse is very similar to the lexical-semantic system that has been revealed by single-word or sentence studies. For example, in one of the earliest neuroimaging studies of narrative speech, Crinion et al. (2003) examined which brain areas were active while adult participants listened to children's stories. The control condition was listening to the story played in reverse, which makes the stories unintelligible while maintaining acoustic complexity and voice qualities of the narrator. When stories were contrasted with reversed stories, there was significant activation in the left ventral IFG and posterior STG, as well as the bilateral ATL extending posteriorly towards the middle temporal gyri and the STG. Following this, multiple neuroimaging investigations of narrative processing have found similar activation patterns (e.g., Awad et al., 2007; Choi et al., 2014; Crinion et al., 2006; Frank & Willems, 2017; Wang et al., 2015; Willems et al., 2016; Xu et al., 2005), with the addition of other regions such as the bilateral AG, MFG, pCi, and medial prefrontal cortex. These areas are well-established parts of the lexical-semantic system. Figure 11.2 shows activation peaks from three such studies. However, relatively coarse contrasts, such as speech versus reversed speech, do not allow for more detailed analysis of how individual semantic features are represented during discourse. Here, more specific analyses will be briefly discussed.

One such study by Wehbe et al. (2014), examined how brain activity was modulated by a set of syntactic, semantic, and discourse-level features while participants read a novel excerpt presented

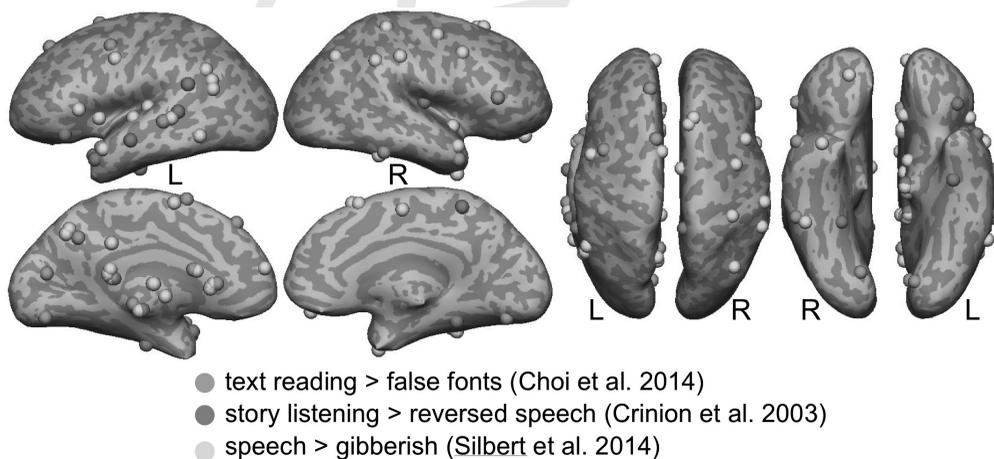


Figure 11.2 Activation peaks from three selected studies

These studies that have reported discourse processing relative to a low-level baseline, such as false fonts or reversed speech. Most peaks represent large surrounding clusters. See e-book for a full-color version of this figure.

word by word. They trained a computational model to predict brain activity in response to a set of 195 features (100 of which were related to semantic content) that were assigned to each word within the story. They found that the semantic features of words were encoded by neural activity in the left IFG and STG as well as the bilateral MTG and AG. At a finer-grained level, they found that words pertaining specifically to physical motions of story characters were represented in the left posterior STG and the left AG (areas implicated in biological motion perception and action), and that the identities of specific characters could be distinguished by activity within the right posterior STG/MTG – an area associated with theory of mind (Saxe, 2006).

In a related study, Huth et al. (2016) recorded brain activity while participants listened to two hours of stories. They trained a model to predict the voxel-wise BOLD signal associated with the semantic features of individual words and found that semantic content of words was encoded by extensive bilateral activity in the frontal, temporal, and parietal lobes. Using dimension-reduction, the words were weighted according to 12 major semantic categories, such as emotional, social, visual, and numeric. Results suggested that the previously mentioned areas of the cortex comprised semantic “tiles,” wherein certain sub-regions are uniquely selective for specific semantic features. For example, areas proximal to the AG were selective for social concepts, while surrounding areas in the parietal cortex were selective for numeric, visual, and tactile concepts. Tiles within the temporal and frontal lobes were selective for other semantic features, such as tactile or violent associations. These semantic tiles were largely consistent across individual participants, demonstrating that either innate neurobiological principals or shared cultural experiences may influence the organization of semantic feature representations in the brain.

This study is an outstanding example of leveraging a large dataset combined with sophisticated analyses to enable examination of lexical semantics during natural speech, for thousands of words simultaneously. A lack of consideration given to potential confounds is a limitation. The authors included only word rate, phoneme rate, and phonemes as covariates. Yet words have many psycholinguistic properties that affect their processing (e.g., frequency, contextual diversity, age of acquisition, associative and taxonomic semantic neighborhoods, phonological neighborhood, to name a few major ones), in addition to many semantic dimensions and other more specialized variables (such as clustering coefficient, biphone/triphone frequency, number of senses, cumulative frequency, and consistency) – let alone their phrase-, sentence-, and discourse-level properties. If such variables are even mildly differentially correlated with semantic categories, the results can be misleading. This is a potential reason why extensive bilateral activation was found in this study, including many perplexing results. For example, it is difficult to explain why the right MFG – an area strongly associated with executive processes such as monitoring and sustained attention – contains a tile representing tactile concepts. Some of the activation, especially in frontal and parietal areas, may represent a mix of conceptual representations, executive processing, and psycholinguistic confounds.

Another important question in naturalistic contexts pertains to how the brain represents and integrates the semantic content of words that are thematically related, but taxonomically dissimilar. For example, in the sentence “the man drank the water,” none of the content words have similar meanings, yet they are thematically related, making the sentence readily comprehensible. In an fMRI study, Frank and Willems (2017) examined this by generating semantic vector representations for each content word from novel excerpts presented auditorily to participants. Within each sentence, the associative semantic distance between the content words and the preceding words was calculated and then correlated with the BOLD signal, controlling for word frequency and surprisal. They found that higher semantic distance was associated with increased activity in the left ATL, the pCu, and the bilateral AG. This suggests that these areas may be involved not only in representing semantic features, but also in the higher-level process of establishing thematic relationships between semantically dissimilar words – for a review, see Mirman et al. (2017).

In a similar vein, during discourse processing, information is sometimes encountered that is not only semantically dissimilar from previous words in a sentence but globally inconsistent with the

information that has been given previously (e.g., a “twist” in a story). Ferstl et al. (2005) examined this as participants listened to stories that provided either chronological or emotional information. Half the stories were globally consistent, while the other half contained a word or phrase at the end that contradicted what had been learned throughout the story (e.g., the first five sentences described a character in a happy situation, but the sixth sentence stated that the character felt sad). Participants were instructed to pay close attention for inconsistencies. By comparing emotional versus chronological conditions regardless of (in)consistency, they found that the pCu, the IPS, and the temporoparietal junction (TPJ) were more active for chronological stories, while the ventromedial prefrontal cortex and the amygdala were associated with emotional ones. This corroborates previous studies showing that certain brain areas are preferentially involved in comprehension depending on the type of semantic information being processed. Then, by comparing consistent versus inconsistent stories at the onset of the target word (collapsed across story type), the authors found that right ATL activity was significantly higher for the inconsistent than consistent condition. This suggests that the right ATL is recruited when encountering unexpected lexical-semantic information, perhaps reflecting increased processing demands when there is a sudden need to update the preceding context.

These studies show how different features of objects or signs, such as perceptual or emotional characteristics, are represented in brain areas that are both information-specific and information-general, and which regions are involved in updating and integrating this information in light of context.

Embodiment

Considerable evidence suggests that conceptual processing relies, at least in part, on brain areas that are involved in physical action or perception (Binder & Desai, 2011), a finding couched in “embodied” or “grounded” theories of cognition. Under this framework, primary or secondary action/perception brain areas functionally contribute to the representation of corresponding semantic features – for example, comprehending action concepts such as “kick” would involve portions of action network (Desai et al., 2015; Johari et al., 2021; Riccardi et al., 2019, 2020). Although many single-word and sentence studies address the relationship between action/perception circuits and conceptual representation, far fewer studies examine this relationship in the context of natural discourse.

Desai et al. (2016) explored the neural correlates of noun manipulability during natural reading using simultaneous eye-tracking and fMRI while participants silently read short passages. Using eye-fixation timepoints, they correlated noun manipulability ratings with the BOLD signal while controlling for number of letters, word frequency, and concreteness. Higher manipulability was associated with greater activity in the bilateral inferior parietal lobe, including the SMG and the AG, as well as the left inferior temporal sulcus. Importantly, these areas have been implicated in the actual use of tools in fMRI and neuropsychological studies. This suggests that, during naturalistic reading, conceptual representation of manipulability recruits action/perception circuits.

Further evidence comes from Birba et al. (2020a), who used transcranial direct current stimulation (tDCS) to examine how stimulation of the primary motor cortex (M1) might affect action-content processing during naturalistic narratives. Participants received tDCS over the left M1, sham stimulation of M1, or stimulation of the left ventrolateral prefrontal cortex. After stimulation, they listened to action texts (ATs, stories that were highly action-related) and neutral texts (NTs, stories lacking action associations), and then answered questions about information either relevant to the verbs in the stories or about circumstances (locative or chronological details). They found that, for the AT condition, M1 stimulation selectively decreased performance in the verb-related questions compared to the circumstantial questions. Importantly, this effect was specific to M1 group (no such effects was found in the other two groups) and it survived after controlling for working memory and vocabulary skills.

In a similar study, this time using electroencephalography, Birba et al. (2020b) recorded brain activity while bilingual participants read ATs and NTs in their first and second languages (L1, L2).

When reading in L1, the AT condition (compared to NT) was associated with increased connectivity between electrodes that have been traditionally implicated in action-related processes. While this group-level effect was not found in the L2 condition, the authors found that greater action-related connectivity for AT was associated with greater L2 proficiency and earlier age of L2 acquisition. These findings suggest that action language processing involves functional connections between action-related brain areas, and that the strength of this connectivity is associated with how consolidated the language is. Taken together, these investigations corroborate single word studies demonstrating a relationship between processing the meanings of linguistic symbols and action/perception circuits, and they show that this relationship remains important for semantic representation even in naturalistic contexts.

Combinatorial and compositional processing

Discourse comprehension requires the combination of smaller symbols into a larger whole at multiple levels. For example, at a relatively low level, individual words must be combined into meaningful phrases. At higher levels, the meanings conveyed through phrases, sentences, and paragraphs must be linked to create a cohesive narrative. Understanding the anatomical organization of how units of information are combined is a vital goal for neurosemiotics, as encountering single words in isolation is relatively rare in everyday life. Here, we briefly review some investigations of the neural bases of combination and composition.

Bhattasali et al. (2018) examined the neural correlates of combination and retrieval at the phrase level using fMRI while participants listened to a story. They used a computational model to identify “multi-word expressions” (MWEs), or word sequences that are better treated as a single unit instead of multiple smaller units that need to be combined. They also used a parser-action counter to measure the compositional complexity of word sequences, with the intention of measuring brain activity associated with having to build a phrase from the bottom up. They hypothesized that MWEs, which may not require as much bottom-up composition, would be associated with memory processes, while composition would rely more on brain areas typically associated with combinatorial processes. After controlling for word frequency and the intensity and frequency of the auditory stimulus, they found that the presence of MWEs was associated with greater activity in the right pCu. Composition, on the other hand, was associated with many brain areas, including the bilateral ATL, IFG, and TPJ, as well as the left posterior STG/MTG and the right AG. In a second analysis, MWEs were rated based on their “cohesiveness” (more cohesive MWEs are more likely to be memorized than less cohesive ones). More cohesive MWEs were associated with right pCu activity, while less cohesive MWEs were associated with left-lateralized AG, MTG, ATL, and IFG activity. pCu is implicated in episodic memory, supporting the authors’ claim that MWE processing is supported by memory. Composition, on the other hand, relies on a variety of areas bilaterally which have been implicated in semantic and syntactic representation and combination.

Brennan and Pylkkanen (2012) investigated compositional processes by using magnetoencephalography to record brain activity while participants read *Sleeping Beauty* (presented one word at a time). Magnetoencephalography is a powerful method for naturalistic language research, as it provides good spatial resolution while also allowing for millisecond-level temporal resolution. They compared activity for words in the narrative condition to a control condition where the words were presented in scrambled order. They found that, for the narrative condition, ATL activity significantly increased 250 ms after word onset, which they attributed to sentence-level compositional and combinatorial processes.

In another investigation of composition, Hsu et al. (2019) used simultaneous eye-tracking and fMRI to study brain activity while participants read passages from scientific texts. They used word order to operationally define the processes of composition and integration. Earlier content words were considered to be important for composition, as they are involved in the initial building of the

meaning of the sentence. Later words were considered to be measuring integrative processes, where new information is added to the context built by previous words. Earlier words were associated with greater activity in the bilateral pCu/pCi, the anterior cingulate (ACC), the right insula, and the left posterior fusiform gyrus. Later words were associated with activity in areas such as the left AG, SMG, and MTG, as well as the bilateral pCu and IFG. This suggests that different brain areas might be more involved in the initial building of the information structure compared to later integrative processes. They also examined neural activity associated with the texts' knowledge structure, a graph theoretical measure of how well associations between concepts are communicated by the text. Texts with optimal knowledge structure allow for more efficient composition and integration of the provided information. Optimal knowledge structure was associated with greater activity in the left MTG, STG, and dorsolateral prefrontal cortex, while suboptimal knowledge structure was associated with greater activity in the bilateral ACC and the left IFG. This suggests that when information is more difficult to combine into a coherent whole, the brain may recruit areas related to executive processes, such as dual-tasking and attention.

Xu et al. (2005) examined how brain activity was modulated as participants progressed through the beginning, middle, and end of a collection of fables presented via text. This allowed for a broad investigation of the neural correlates associated with synthesizing narrative elements into a coherent whole. By comparing the beginning of the story to the control condition of randomly presented words, they found that initial story composition was associated with a largely left-lateralized network of regions including the IFG, the ATL, and the AG. However, when directly contrasting the end of the story with the beginning, they found that the activity had shifted to become more bilateral, including areas such as the right ATL, AG, pCu, and IFG. This suggests that, as narrative elements are integrated into a complete story, right hemisphere areas are recruited to aid in the possibly richer representation of the narrative and connect it to prior experience, knowledge, and beliefs.

These studies explored how the brain combines and integrates linguistic symbols at phrase, sentence, and narrative levels. At the phrase level, different brain areas are preferentially recruited depending on whether the phrases are very common or fixed (likely relying on memory processes) or more unique (requiring meaning to be built from the ground-up). At sentence and narrative levels, different brain areas are more involved in processing early information, when the sentence or story is first being built, compared to later information, which requires integration to the already existing knowledge structure.

Regions involved in semantics of discourse processing

As we have seen, many cognitive processes are required to successfully make meaning from linguistic symbols in naturalistic contexts, ranging from relatively low-level lexical-semantic retrieval of single words, to combinatorial processes, all the way up to higher-level functions such as contextual integration, creation of situation models, and inferring thoughts, emotions, and motivations of actors within the narrative. Several brain regions are consistently implicated in the semantics of naturalistic discourse processing and can be thought of as neurosemiotic "hubs." We now discuss possible roles of these regions, relating them to cognitive processes involved in interpretation of signs.

Anterior temporal lobe

The ATL is one of the most common regions activated during naturalistic language processing. A large body of research implicates the ATL in lexical access (Mesulam et al., 2013), semantic knowledge (Lambon-Ralph et al., 2017), combinatorial processes (Brennan et al., 2012), and social-emotional processing (Olson et al., 2013), all of which are part of discourse comprehension. Given the previously discussed evidence, it is possible that the ATL plays a special role in combining and integrating lexical-semantic information, perhaps especially so when that information is unexpected

or difficult to synthesize. Naturalistic language studies have found that ATL activity is associated with high surprisal (Willems et al., 2016), semantic distance (Frank & Willems, 2017), and compositional demands (Bhattasali et al., 2018) at the sentence-level. The right ATL was also activated in response to encountering a word that was inconsistent with the previous context (Ferstl et al., 2005). All of these processes required the combination and integration of new, and sometimes unexpected, lexical-semantic items into an existing context.

The ATL has also been implicated in syntactic structure building (e.g., Brennan & Pyllkanen, 2012, 2017). For example, using magnetoencephalography, Brennan and Pyllkanen (2017) found that ATL activity was associated with the amount of syntactic structure being processed during naturalistic listening – see also Henderson et al. (2016). The investigation of composition by Bhattasali et al. (2018), discussed previously, could also be interpreted as measuring syntactic structure building, as their measure of composition was parser-action count. However, as noted by Brennan et al. (2012), it is difficult to disentangle syntactic from semantic processes during natural language comprehension, given that as syntactic structure is being built, semantic content is also being processed.

Here we briefly suggest a novel hypothesis: that the role of lateral ATL in language processing is *lexical* rather than semantic or syntactic. ATL may represent units that connect (orthographic and phonological) lexical forms to their meaning. It contains both long-term and short-term memory (STM) for unique items (such as words). This hypothesis can explain why unexpected or semantically distant words lead to greater activation in ATL, as the prior context needs to be kept active longer in STM in order to re-evaluate and integrate the unexpected item. This interpretation is also consistent with the syntactic structure building account, as new nodes in the syntactic tree place greater demands on STM. At the discourse level, STM is used to link various components of discourse and for anaphora resolution, leading to greater involvement for discourse over sentences. This hypothesis differs from the semantic hub view in that, for our account, the ATL is not responsible for storing coherent concepts themselves, but instead points to the distributed semantic representations elsewhere. Deficits in language tasks after ATL damage arise from impairments in *access* to semantic content rather than to semantic content itself. Thus, the ATL is a critical neurosemiotic hub that connects the sign to its object (or what is signified), when the relationship between the two is largely arbitrary or symbolic. This hypothesis awaits further experimental examination.

Angular gyrus

The AG is another important part of the neurosemiotic system. This structure has been implicated in functions such as semantic representation, especially for concrete concepts (Wang et al., 2010), as well as episodic memory and attention – for a review, see Seghier (2013). It is also part of the default mode network (DMN), a group of brain areas that are active when participants are at “rest” (i.e., not actively attending to stimuli or performing an explicit task in the scanner). Interestingly, DMN activity has been attributed to mind-wandering or daydreaming (Kucyi & Davis, 2014) and has a large contribution from semantics, as participants may be thinking about past, future, or hypothetical events, including people, objects, and relations in the events. This is a state of mind that shares many similarities with naturalistic language processing.

Naturalistic language studies suggest that the AG may serve as a high-level semantic convergence zone that not only represents specific semantic features, but might also prime semantic representations, including events that engage mechanisms elsewhere in the brain (Binder & Desai, 2011). Evidence that the AG subserves processing of specific semantic features in discourse comes from Desai et al. (2016) and Wehbe et al. (2014), who found that AG activity was associated with noun manipulability and physical motions of characters, respectively. Other studies provided evidence that the AG is involved in semantic representation at an even higher level. For example, Wehbe et al. (2014) demonstrated that the AG encodes semantic features of words, while Desai et al. (2020) and Willems et al. (2016) associated AG activity with the representation of rich semantic contexts,

larger semantic neighborhoods, and priming of the larger semantic system when upcoming words are strongly predicted. This also meshes with its role in representing thematic relationships between concepts (Schwartz et al., 2011). Frank and Willems (2017) found that AG activity was associated with words that were semantically dissimilar from previous words in the sentence, a situation which would require thematic relationships to be built between semantically unrelated concepts (e.g., *the man drank the water*). Additionally, studies showing that AG activity increases towards the end of sentences (Hsu et al., 2019) or stories (Xu et al., 2005) could be interpreted as evidence of greater thematic processing, or “semantic structure building,” as more complex relationships between characters or concepts are established. Thus, AG may have role in integration of distributed features to form coherent lexical concepts, as well as integration across time spanning phrase, sentence, and discourse-level scales to form event concepts.

Precuneus and posterior cingulate

The pCu and pCi are frequently activated but less well understood hubs of conceptual activity. They are sensitive to lexical semantic variables such as concreteness (Binder et al., 2009), but are also active during higher-level processes such as daydreaming, internally-directed cognition, episodic memory, emotion, and theory of mind – for reviews, see Cavanna and Trimble (2006) and Leech and Sharp (2014). They are also part of the DMN and are highly functionally connected to multiple brain networks. This has led to suggestions that these areas are involved in “tuning” or coordinating activity in distributed areas of the brain. It is possible that in naturalistic language processing, the pCu and pCi are involved in building and maintaining “situation models,” which comprise information about characters, events, and settings within the discourse (Kemmerer, 2021). Support for this account comes from studies demonstrating that these regions become more active as sentences and stories progress (Hsu et al. 2019; Xu et al. 2005), perhaps reflecting the updating of situation model content. Activity in these regions is also associated with “event boundaries” in narratives, where information about characters, time, events, and locations is changed (Speer et al., 2007). Further evidence comes from Ferstl et al. (2005), who found that the left pCu was activated in response to stories containing chronological information, which is an important part of the situation model. Two functional divisions of the pCu/pCi territory have been suggested (Cavanna & Trimble, 2006). The anterior section, including the pCi and retrosplenial cortex, would be associated with mental imagery and spatial navigation especially for egocentric processing, with higher activation for concrete concepts. The posterior region would be more involved in episodic memory retrieval, exhibiting greater activity for abstract concepts (Desai et al., 2018b). Thus, this large territory as a whole may play a central role in updating situation models involved in discourse, through episodic memory with both concrete/spatial and abstract components. A better understanding of how the pCu and pCi are involved in building and integrating linguistic symbols into situation models will be important for a complete neurosemiotic model.

Bilaterality

Although it is agreed that the brain’s language systems are at least partially bilateral, most traditional language studies find largely left-lateralized activity with limited involvement of the right hemisphere (Binder et al., 2009), and neuropsychological studies have shown that patients with right hemisphere brain damage usually have better language-related outcomes than those with left hemisphere damage. In contrast to these observations, many of the investigations described above found highly bilateral activity associated with naturalistic language processing. This raises the important question of how the right hemisphere is contributing to discourse comprehension (Beeman & Chiarello, 2013).

One possibility is that the right hemisphere is contributing to “paralinguistic” processes – that is, aspects of communication that are not directly related to language. For example, research has shown that the right hemisphere is involved in nonverbal semantic processing, speech prosody, pragmatics (use of language in context), and understanding subtle linguistic or social cues (Lehman Blake et al., 2013). Paralinguistic information is an important part of effective communication, and hence is important for understanding how different types of signs contribute to meaning-making. These paralinguistic processes could be expected to play a more significant role in naturalistic language than in single-word or sentence studies, leading to greater bilateral activity. Another possibility, as suggested by Ferstl et al. (2005), is that the right hemisphere is recruited in response to increased processing demands associated with naturalistic language processing. Under this hypothesis, the heightened conceptual, compositional, and integrative demands of discourse lead to the activation of homologous right hemisphere areas to support functions that usually could be handled by the left hemisphere. Future studies should seek to reveal how right hemisphere areas functionally contribute to the neural representation of signs, their objects, and their interpretations.

Neurosemiotics and language in the wild

The studies discussed here represent initial steps into the neurosemiotic quest for understanding brain bases of representation and processing of signs. The “good news” is that, at least for some psycholinguistic variables, the wealth of insight that has been accumulated from studies of relatively isolated signs and symbols is applicable to their processing in naturalistic contexts as well. At the same time, the evidence from the naturalistic language research discussed in this chapter can both inform, and be informed by, neurosemiotic perspectives of meaning and comprehension. Perhaps most significantly, the findings help delineate the neuroanatomy of specific semiotic processes, such as connecting the sign to its object, representing and interpreting the meaning of the object, and combining smaller symbols into a coherent whole. These anatomical findings also give credence to a holistic and dynamic view of symbol processing, much in line with neurosemiotic perspectives. That is, the results show that the anatomical representations of symbol processing change dynamically within the larger context of a narrative, due to complex interactions between many different types of signs and symbols (i.e., both linguistic and paralinguistic).

Naturalistic language research in cognitive neuroscience, on the other hand, can be informed and inspired by the more holistic neurosemiotic perspective. Traditional neuroscientific research tends to be highly modular, with the goal of investigating a single, specific process (e.g., syntax, semantics). Conversely, semiotic perspectives underscore the fact that these processes interact with each other in dynamic, highly complex ways in order to build meaning out of a combination of linguistic, paralinguistic, and social/contextual signs and symbols. A clear goal for the field is to delineate how these factors influence the ways in which the brain represents meaning.

Cautions, caveats, and future directions

Naturalistic language research is essential for a more complete understanding of neurosemiotics. However, similar to single-word studies, it comes with inherent limitations and difficulties, which must be addressed. First, it is difficult (and sometimes impossible) to disentangle specific cognitive processes, including the broad categories of syntax and semantics, and many sub-processes within, when using naturalistic stimuli. This limits the strength of conclusions that can be drawn pertaining to the contributions of individual brain areas. Relatedly, using low-level control conditions such as reversed speech or pseudoword passages allows for only coarse conclusions regarding discourse processing, and does not shed light on specific components of this process. When examining any particular

component of meaning, the issue of confounds and correlated variables is also non-trivial. The number of psycholinguistic variables that affect processing of just single words is virtually unlimited. Over 200 psycholinguistic variables are currently known and have been used, and this list is continually increasing. It can be argued that the traditional approach of studying a particular variable by matching conditions on all other variables is misleading and provides a false sense of security, because there are always other variables that are not accounted for. Some argue that the solution to this problem is to collect a large amount of data and not worry about controlling for potential confounds. We disagree with such an approach, which advocates for simply ignoring confounds. It is true that perfect matching of lexical (or phrase and sentence level) variables is virtually impossible; however, it does not mean that not accounting for any or few variables is somehow better than controlling for as many major variables as possible. Through decades of psycholinguistic research, several salient lexical variables have been identified (e.g., frequency, contextual diversity, letter and phoneme length, consistency, and imageability/concreteness, as well as orthographic, phonological, and semantic neighborhoods). Further contributions come from sentence and discourse-level variables, such as surprisal and entropy, verb argument structure, and sentence type. This knowledge from past research should be used while acknowledging that any list of variables is never complete. Collecting large amounts of data can ensure that words typically occur in multiple contexts, and this can limit effects of any specific context. However, this does not automatically solve the problem of confounds. If anything, it can exacerbate it, because with a large n , even small correlations become significant. Control conditions with randomized sentences and word lists (as opposed to nonspeech or similar low-level controls) can possibly provide a better “out” from the conundrum of matching for psycholinguistic variables.

The study of naturalistic language is advancing in a number of fruitful directions – see Newman-Norlund et al. (2021) for a description of an ongoing, large-scale investigation that includes discourse and naturalistic language measures. These include: (1) better control for lexical and sentence-level variables either through randomized presentation or matching; (2) combining methods to leverage their unique strengths (e.g., fMRI and eye-tracking, or fMRI and electroencephalography); (3) carefully manipulating discourse content to isolate specific components of discourse processing; (4) studying structural and functional connectivity and its modulation during discourse; (5) studying oscillatory activity at different time scales; and (6) using brain stimulation methods to address roles of specific regions in discourse processing. Studies that use naturalistic materials, while certainly being demanding, promise to pay rich dividends in advancing neurosemiotics.

Conclusion

In this chapter, we have provided a brief review of neuroscientific studies investigating how the brain derives meaning from language in naturalistic contexts, a question at the heart of neurosemiotics. The findings revealed a distributed network of brain areas that work together dynamically to build, maintain, and update information communicated via naturalistic language. Viewing this research through the holistic perspective of semiotics reveals exciting new directions for investigations devoted to the neural representations of meaning. A goal of the field is to pioneer novel methods and experiment designs to shed light on the complex interplay between linguistic, paralinguistic, and social/contextual information in the brain, which will provide a more complete understanding of the biological bases of meaning in the wild.

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