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FEATURE ARTICLE

The Brain's Language

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EDITOR'S NOTE

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The Brain's Language

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1. Introduction

Language affords human beings an incredible degree of representational flexibility. Although languages are made up of a limited number of speech sounds, those sounds are grouped and ordered within any given language to create a much larger set of possible words. And, although there may be a limit to the number of individual words people can store in long term memory and have readily at their disposal at any given moment, words can be combined to form an infinite number of sentences describing real, imaginary, and impossible objects and events, as well as emotions and countless other notions.

Especially striking is that most humans learn this complicated coding system early in life and use it throughout their lifespan with ease. Every day, humans produce and comprehend completely new strings of words, at a rate of about 150 words per minute (Maclay & Osgood, 1959). This degree of flexibility and efficiency is a consequence of the structure of language together with the structure of the entity that mediates language processing, the human brain. Here we examine how these come together in cognitive electrophysiological studies of language.

1.1 The structure of language

Linguists typically describe language as a system with several levels of embedded structure. Phonetics is the study of the speech sounds that are utilized by all human languages; it provides a means for describing how those sounds are produced, transmitted, and perceived. For speakers of any given language, sounds (and hand shapes in signed languages) come to be systematically organized, categorized, and interpreted. That is, various combinations of different actual sound patterns (mediated by measurably different vocal tract configurations) may all yield a sound that an English speaker interprets as a "t" -- the (different) sounds in the words "top", "stop", "pot", and "button", for example. Phonology is the study of the sound patterns and systems of human language and the kind of knowledge that

people have about the sound patterns of their particular language.

Combinations of phonemes that have come to have their own meaning are known as "morphemes". Some morphemes are whole words (e.g., "cat"); others are affixes whose meaning serves to modulate the meaning of whole words (e.g., the /s/ which, when added to the end of an English word, makes that word plural). Morphology, then, is the study of the patterns that govern word formation, including both how new words/morphemes are created (derivational morphology), and how existing morphemes are combined to create different forms of the same word (inflectional morphology).

Just as morphemes are combined to create new words and new forms of words, whole words are combined to make larger units of language -- phrases, clauses, sentences, and discourses. Within and across languages, the way in which certain words and types of words come to be put together to create these larger language units is patterned. Phrases are built around particular types of words. Noun phrases, for example, may contain several different types of words but must contain at least one noun and must not contain a verb. In many languages, the kinds of words that occur in a phrase also come in a certain order. In English, a noun phrase will typically consist of a determiner (a, the) followed by one or more adjectives, followed by the noun. In Italian, in contrast, the determiner (un, il) is typically followed by the noun, and the adjectives, if any, often come last. Phrases themselves act as units that can be found in multiple places in a sentence -- for instance, noun phrases may be subjects, objects, or parts of prepositional phrases. This study of sentence structure is known as syntax.

Ultimately, humans use language to transmit specific information -- meaning -- that depends not just on the general pattern of sounds or words, but on the specific words used, their specific pattern, and the specific context in which they occur (linguistic, social, environmental). The study of language meaning in general, semantics, and of meaning in its larger context, pragmatics, asks how language is used to transmit and, in some cases, distort reality.

Thus, investigations of human language reveal multiple levels and types of structure that may help explain how language can be used so readily and efficiently. However, it cannot be the structure of language alone that makes it such an efficient and useful tool, for if that were the case it would be difficult to understand why humans alone come to have fully-developed language skills. Rather, it must be the structure of language in combination with that of the human brain which explains how humans acquire, use, and create language. The question that then arises is: does the human brain "see" language the way that linguists see language?

1.2 Neural communication: brain functioning and language

In part, the answer to this question is certainly "yes". At some level the brain probably does process phonological patterns differently than syntactic or semantic patterns, and there is likely to be some difference between the brain's processing of two different sounds that are ultimately treated alike and two that are ultimately distinguished. Many of the patterns described by linguists likely correspond to meaningful differences in brain processing. On other levels, however, the answer must certainly be "no". Linguists examine language competence as opposed to performance; they are generally not concerned with processing issues and thus often examine patterns collapsed across time and space. However, the brain's processing of language necessarily takes place in time and space, and both are likely to be important. For example, linguistic inputs that are separated by different stretches of time or that require different numbers/sizes of saccadic eye movements are likely to be treated differently by the brain -- though not, perhaps, by linguists. At the same time, not all differences noted by linguists are likely to be meaningful to all brain areas at all times. Early in visual processing, for instance, the brain responds similarly to letter strings that can be pronounced (i.e., are phonologically legal) and those that cannot (i.e., illegal strings).

The brain not only represents language but also is involved in its creation and its real time use. To understand how requires knowing something about the brain and about what regularities in language the brain notices and under what circumstances. Thus, cognitive neuroscientists interested in language processing have turned to a number of noninvasive brain imaging techniques in order to get a picture of the brain in action as it processes language. This chapter reviews one such technique that provides a direct measure of brain activity with exquisite temporal resolution.

1.3 The physiology of event-related brain potentials (ERPs)

Among the various kinds of brain signals that can be monitored noninvasively, the most direct and immediate are electrochemical. Comprehending and producing language are

brain functions that require the coordinated activity of large groups of neurons. This neural communication takes place via wave-like changes in the electrical potential along neurons and their processes (dendrites and axons). Under normal (non-stimulated) conditions, each neuron has a "resting" electrical potential that arises due to the distribution of positive and negative elements (ions) inside and outside it. Stimulation of the neuron changes the permeability of the neural membrane to these charged elements, thereby altering the electrical potential. A transient increase in potential (depolarization) at the cell body can cause an all-or-none "action potential", a wave of depolarization that moves along the cell's axon. The action potential can then be spread to other neurons via the release of chemicals (neurotransmitters) from the axon tip that travel in the extracellular space and cause permeability changes in the dendrites of nearby neurons. These permeability changes may cause an action potential in the receiving cell as well, or may simply alter the electrical potential of that cell such that it will be more or less sensitive to other stimulation.

Neural communication thus involves the flow of charged particles across neural membranes, which generates an electric potential in the conductive media inside and outside the cell. These current flows are the basis for electrophysiological recordings in the brain and at the scalp surface, as changes in electrical potential can be monitored by placing at least two electrodes somewhere on the head (or in the brain) and measuring the voltage difference between them. The resulting electroencephalogram (EEG) observed at the scalp is due to the summed potentials of multiple neurons acting in concert. In fact, much of the observed activity at the scalp likely arises from cortical pyramidal cells whose organization and firing satisfies the constraints for an observable signal (see, e.g., Kutas & Dale, 1997, for more detail).

The EEG measures spontaneous, rhythmic brain activity occurring in multiple frequency bands. For the purposes of understanding the neural basis of language processing, however, we are often interested in the brain's response to a particular event or kind of event, such as the appearance of a word on a computer screen. To examine event-related activity in particular, one can average the EEG signal time-locked to the stimuli of interest to create an "event-related potential" or ERP. The ERP, then, is a waveform consisting of voltage fluctuations in time, one waveform for each recording site. This waveform consists of a series of positive and negative-going voltage deflections (relative to some baseline activity prior to event onset). Under different conditions, one might observe changes in the morphology of the waveform (e.g., presence or absence of certain peaks), the latency, duration, or amplitude (size) of one or more peaks, or their distribution over the scalp. Until recently, electrophysiological investigations of language have focused on relatively fast (high frequency), transient ERP responses; more recently, however, slower potentials that

develop over the course of clauses and sentences have also been monitored.

ERPs are useful measures for the study of language processing because they are a continuous, multidimensional signal. Specifically, ERPs give a direct estimate of what a significant part of the brain is doing just before, during, and after an event of interest, even if it is extended in time. And, they do so with millisecond resolution. ERPs can indicate not only that two conditions are different, but also how – whether, for example, there is a quantitative change in the timing or size of a process or a qualitative change as reflected in a different morphology or scalp distribution. To a limited extent, ERPs can also be used to examine where in the brain processes take place (via source modeling techniques and in combination with other neuroimaging techniques; for more information see review by Kutas, Fedemeier, and Sereno (1999)).

Using ERP techniques, researchers have looked at language processing from early stages of word recognition through the processing of multi-sentence discourses, from the planning of a speech act to its articulation (e.g., Kutas & Van Petten, 1994; Osterhout, 1994; Osterhout & Holcomb, 1995). In doing so, one finds that the brain's processing of language involves many different kinds of operations taking place at different times and different temporal scales. These operations differ in the extent to which they are general purpose or more specific to language, in the extent to which they are affected by context (and what type of contexts they are sensitive to), and in the extent to which they interact with one another in space and time.

2. Language comprehension

Initially, the brain cannot know whether an incoming stimulus is linguistic or not. Thus, its first task when confronted with a written, spoken, or signed word -- as with any external, perceptual stimulus -- is to determine what it is, or at least to what categories it might belong. This decision is crucial and difficult; in order to process a stimulus effectively, attention must be distributed over the stimulus appropriately, certain kinds of feature information must be extracted and possibly stored into memory, information needed to interpret the stimulus must be accessed from long-term memory, and so on. Since the brain cannot not always know what kind of stimulus it will encounter at any given moment, some aspects of (especially early) perceptual processing are likely to be similar regardless of the nature of the stimulus. At times, processing decisions may also be guided by guesses -- based on frequency, recency, and other predictive regularities -- about what the stimulus is likely to be. When it can, it seems that the brain makes use of both top-down (expectancy or context-based) and bottom-up (stimulus-based) information to guide its analysis of input. Thus, if

someone has been reading or listening to a stream of linguistic stimuli, their brain might be biased to treat incoming input as linguistic; in other contexts, the same input may initially be interpreted as non-linguistic (e.g., Johnston & Chesney, 1974). To the extent that the context allows, the brain might also form expectations about the physical nature of the stimulus -- color, size, font, loudness, voice, etc. Modulation of attention to such stimulus parameters is reflected in variations in the amplitude of early sensory components such as the P1 and N1 as well as the Nd and processing negativity (see relevant chapters in this book); violations from such expectations in the auditory modality are seen in the MMN. Depending on the task demands, there may be effects on later cognitive ERP components such as N2, P3, etc.

2.1 From input to meaning

Regardless of the nature or degree of available top-down information, however, the first task for successful language comprehension involves early sensory classification of stimuli. In the visual modality, for example, this might include differentiating single object-like stimuli from strings, orthographically legal words from illegal words, or pseudowords from nonwords. Schendan, Ganis, and Kutas (1998) examined the time course of this type of classification by comparing the ERP responses to object-like (real objects, pseudo-objects), word-like (words, letter strings, pseudo-font strings), and intermediate (icon strings) stimuli. Around 95 millisecond a negativity (N100) over midline occipital sites distinguished single object-like stimuli from strings. This differentiation is important because, as supported by the neuropsychological literature, different attentional resources are required to process sets of spatially distinct objects as opposed to a single, spatially contiguous form, and these processes are mediated by different brain areas (e.g., Farah, 1990). This classification was followed shortly by a distinction between strings made from real letters (words and pseudowords) and those made from other characters (icon strings, pseudo-font), suggesting that the visual system of experienced readers has developed the ability to rapidly detect physical stimuli with the properties of real letters. A distinction between words and pseudowords followed, beginning approximately 200 milliseconds post-stimulus-onset. Similar time- course of analyses and categorizations seem to hold for auditory inputs as well; for example, the ERPs to meaningful and nonsense words are very similar within the first 150 milliseconds of processing and begin to be distinguishable by 200-250 milliseconds (Novick, Lovrich, & Vaughan, 1985).

Although ERPs provide a very temporally-precise means of determining the latest time by which the brain must have appreciated the difference between two conditions or stimuli, they do not provide a clear way of telling what that difference means nor the extent to which information about that difference will be available or used in further

processing. So, the fact that the processing of real and pseudowords is differentiated at some level by 200-250 milliseconds does not necessarily mean that the brain has identified one type of stimulus as a word and the other as not a word (in the same way that a linguist or psycholinguist might). Rather, the brain may have had more exposure to one class of stimuli than the other or have appreciated the fact that one stimulus class contains more unusual (infrequent) letter combinations. In fact, pronounceable pseudowords continue to be processed much like real words (in terms of the components elicited, though not necessarily in their size and latency) for several hundred milliseconds more. Unlike nonwords, but like "meaningful" stimuli including real words, pronounceable pseudowords elicit a negativity peaking approximately 400 milliseconds post-stimulus-onset (N400). So, it would seem that at least some of the processing circuits of the brain deal with pseudowords, which have no particular learned meaning, no differently than they do with real words for some time after an initial differentiation. Perhaps the early differentiation has less to do with "words" versus "not words" and more with the extent of prior exposure. ERP research with children just acquiring language and/or reading skills as well as with adults learning a second language may provide a means for examining this hypothesis (Mills, Coffey-Corina, & Neville, 1997; Neville et al., 1997; Weber-Fox & Neville, 1996). Indeed, answering such questions poses one of the major challenges in cognitive neurolinguistics.

It is around the time that the brain's response to words seems to first deviate from that to pseudowords that the ERP also shows a sensitivity to a word's frequency of occurrence in a given language (Francis & Kucera, 1982) -- or, from the brain's point of view, the context-independent probability of encountering a particular word. King and Kutas (1998b) found that the latency of a left anterior negativity (which they labeled the lexical processing negativity, or LPN) occurring between 200 and 400 milliseconds post-stimulus-onset is strongly correlated with a word's frequency of occurrence in the language. In short, the brain seems to process more rapidly words that it has had more experience processing. This kind of early difference in the speed with which words are processed can have large consequences later in the processing stream. King and Kutas (1998b) suggested that at least some of the reported differences between the processing of so-called "open class" (nouns, verbs, adjectives, adverbs) and "closed class" (determiners, articles, prepositions) words was due to differences in their average frequency and the consequences this had on their early neural processing (also see Osterhout, Bersick, & McKinnon, 1997a).

It is important to point out, however, that there is no single time or place where "word frequency" is processed and/or stored. Rather, word frequency affects multiple stages of processing including word identification, access of associated phonological or semantic information from long

term memory, maintenance of word form or associated information in working memory, etc. In fact, ERP results clearly demonstrate that word frequency has different effects later in a word's processing. For example, with all other factors held constant (especially in the absence of semantic context), N400 amplitude is an inverse function of word frequency (Van Petten & Kutas, 1991). As will be discussed later, the N400 seems to be related to the access of semantic information from long term memory and/or the integration of this information into a larger context. This stage of processing is also affected by more "immediate" or local frequency information -- namely, repetition in the experimental context (e.g., Rugg, 1985). Similar to the effects of global frequency information, repetition reduces the amplitude of the N400 activity, among other components (Van Petten, Kutas, Kluender, Mitchiner, & McIsaac, 1991).

2.2 Processing patterns

The fact that a word is encountered frequently or was just encountered thus affects the way it is processed by the brain. Moreover, it affects processing at different times and most likely in different ways; the time interval since the last repetition, the number of repetitions, and the context within which the repetition occurs all matter (Besson & Kutas, 1993; Besson, Kutas, & Van Petten, 1992; Young & Rugg, 1992). Effects like these are likely to hold for language units larger than words -- e.g., frequent and infrequent word combinations, frequent or infrequent syntactic structures, etc. In fact, ERP data suggest, for example, that the brain is sensitive to the probability of the relationship between a pronoun and its antecedent. When an occupational title (e.g., "secretary") is paired with the more "probable" (by US census data) pronoun "she", less negativity is observed around 200 milliseconds over left anterior sites (LAN) than when the same occupation is paired with the less probable pronoun, "he" (King & Kutas, 1998a). In the latter case, the brain may assume that the "he" refers to a new participant since the pronoun-antecedent pair seems less likely; the increased negativity may then reflect the working memory load associated with holding onto information about two participants as opposed to only one. In a somewhat similar design with reflexive pronouns, Osterhout, Bersick and McLaughlin (1997b) found that pronouns that disagreed with gender definition or gender stereotype of an antecedent noun elicited a large positivity (i.e., the P600 typically associated with syntactic violations). The important point, however, is that pronouns elicit reliable ERP effects that can be used to investigate the link between them and the nouns to which they refer -- a link that clearly relies on working memory.

Probability may also play an important role in the brain's processing of syntactic aspects of a sentence. Various types of syntactic violations have been found to elicit a late positivity called the P600 or the syntactic positive shift (SPS) (e.g., Coulson, King, & Kutas, 1998b; Hagoort,

Brown, & Groothusen, 1993; Neville, Nicol, Barss, Forster, & Garrett, 1991; Osterhout & Holcomb, 1992). This positivity has a variable onset latency (generally late) and a midpoint around 600 milliseconds -- though this may vary with the complexity of the linguistic structure involved (Munte, Szentkuti, Wieringa, Matzke, & Johannes, 1997). Its distribution is most often posterior, though anterior effects have also been reported. The P600 is typically observed when some aspect of the sentence's structure violates the rules of the language -- for example if subjects do not agree with their verbs in number ("they is"), if pronouns have the wrong case ("the plane took we to Italy"), or if items are out of order within phrases ("Max's of proof the theorem"). It is important to note, however, that the P600 is not contingent on the presence of a grammatical violation; it is also elicited by points of processing difficulty, where the difficulty stems from processing at a grammatical or structural level. Although these manipulations are all "syntactic" to linguists, they differ significantly from one another in ways that are likely to matter to the brain -- for example, some, like the phrase structure violations, rely on word position while others, like subject-verb agreement, depend on the relationship between words relatively independent of position.

So what might the P600 be indexing? A clue comes from recent work by Coulson, King, and Kutas (1998b) that examined the response to syntactic violations (specifically pronoun case and subject-verb agreement violations) when these violations were either frequent or infrequent in an experimental run. They observed a P600 response to ungrammatical as compared with grammatical trials, although infrequent ungrammatical events elicited larger P600s than frequently occurring ungrammatical events. Moreover, even grammatical events elicited some P600 activity when they occurred infrequently among many ungrammatical sentences (for further discussion see Coulson, King, & Kutas, 1998a; Gunter, Stowe, & Mulder, 1997; Munte, Heinze, Matzke, Wieringa, & Johannes, 1998a; Osterhout & Hagoort, 1999; Osterhout, McKinnon, Bersick, & Corey, 1996).

It seems, then, that the part of the brain that is sensitive to syntactic violations is also sensitive to the probability of those violations. Note that the P600 is not typically elicited by semantically improbable events. Rather, it seems to be most reliably elicited by and responsive to the probabilities of morphosyntactic patterns of various kinds. This may suggest that, at least at some point, the processing of syntax takes place by reference to the relative (perceived?) frequency of various regularities in the language, a frequency that is continuously updated with experience. Much work still remains to be done detailing the sensitivity of P600 amplitude to non-linguistic variables.

2.3 Meaning and memory

These observations suggest that the brain is sensitive to the frequency and recency of exposure to particular patterns.

Its sensitivities range from the probability of encountering a particular physical stimulus to the probability of those stimuli patterning in a particular way with respect to one another in a phrase or sentence. These last results also highlight another important aspect of language, namely, the need to process relations between items, at different levels of abstraction. In particular, to make sense of linguistic input the brain needs (1) to relate various types of words with one another and (2) to relate words and groups of words with real-world knowledge stored in long term memory. Language-related ERP research has been directed at delineating the time-course of the processes involved in solving the mapping and integrative problems raised by each of these needs.

Many linguistic patterns emerge over the course of multiple words separated by time and/or space, depending upon the modality of presentation. Processing relations between these items necessitates that the brain maintain them in some kind of temporary store or "working memory". Even simple, declarative sentences (e.g., "John really likes his pet dog.") require working memory resources. At minimum, "John" must be held in memory so that the reader/listener knows who is being referred to when the pronoun "his" is encountered. Some information about "John" being a singular subject must also be held in working memory in order to know that "likes" but not "like" is the correct verb form, and so on. While all sentences tap into working memory, some clearly require more working memory resources than others. For instance, a sentence containing a relative clause (e.g., "The reporter who followed the senator admitted the error") typically requires more working memory resources than a simple declarative sentence, in part, because a participant ("the reporter") is involved in two clauses/actions ("following" and "admitting"). These "subject-relative clauses" (so called because the subject is the same in both the main clause and the relative clause), however, are presumed to require fewer working memory resources than object-relative clauses like "The reporter who the senator followed admitted the error". In object relative clauses, the subject of the main clause ("the reporter") must be kept distinct from the subject of the relative clause ("the senator").

By examining sentences that vary in the extent to which they require working memory resources, one can examine the nature of the brain's response to working memory load (e.g., Friederici, Steinhauer, Mecklinger, & Meyer, 1998; King & Kutas, 1995; Kutas & King, 1996; Mecklinger, Schriefers, Steinhauer, & Friederici, 1995; Muller, King, & Kutas, 1997). In addition, one can assess individual variation in the brain's response to sentences of varying structural complexity as a function of the amount of working memory resources available (e.g., comparing individuals with high versus low working memory "spans" with those who have less working memory resources). For example, King and Kutas (1995) compared ERP responses to subject and object relative sentences read one word at a

time. Good comprehenders elicited greater left, frontal negativities to the second noun phrase ("the senator") in the object relative as compared with the subject relative clauses. This is the point in the sentence where, in the case of object relatives, a second subject must be stored in working memory. In contrast, the response of poor comprehenders (with less working memory resources) was quite negative to both types of sentences; thus, both types of sentences seemed to tax working memory resources for poorer comprehenders. Similar effects were observed for these same sentences presented as natural speech (Muller et al., 1997). These results led to the hypothesis that the left anterior effect reflects general, as opposed to modality specific, working memory operations. A similar left anterior negativity (LAN effect) has also been observed for wh-questions (Kluender & Kutas, 1993). In English wh-questions (e.g., "Who did the doctor cure ___?"), the wh-element (the "filler", in this case the word "who") appears at the beginning of the sentence leaving a "gap" in the canonical word order (which in English is subject-verb-object). Another example comes from uncommon (and therefore difficult) word orders in German (Roesler, Pechmann, Streb, Roeder, & Hennighausen, 1998). The role of working memory operations in sentence processing can also be examined by simply adding an irrelevant or elaborative clause to simple transitive sentence (Gunter, Jackson, & Mulder, 1995).

The extended nature of various working memory operations is also manifest in less transient, slow potential effects (long lasting potentials on the order of seconds). For example, in response to the subject versus object relative clauses discussed above, good comprehenders show a slow positive shift to the subject-relative sentences over frontal sites that lasts for the duration of the relative clause and beyond; poor comprehenders do not show either this slow positivity or this difference (Kutas & King, 1996). This comprehension-related ERP difference shows up even for simple transitive sentences, with good comprehenders generating much more of a frontal positive shift than poorer comprehenders. At the same time, poorer comprehenders show enhanced early sensory visual components such as the P1-N1-P2 relative to the better comprehenders. This suggests that poorer comprehenders may have devoted more resources to lower-level perceptual processing than good comprehenders, thereby having fewer resources to devote to higher-order (possibly working-memory demanding) language processes. The potentials in normal elderly individuals for both simple transitive and object relative sentences most resemble those of the poorer comprehending younger individuals (Kutas & King, 1996).

In general, these sets of results support claims originally made in the behavioral literature that successful language comprehension involves the storage and retrieval of information into working memory (e.g., Carpenter & Just, 1989; Daneman & Carpenter, 1980; Daneman & Merikle, 1996). Only through the use of working memory can the

brain process critical relationships between sensory stimuli distributed over time and space. In addition, these results suggest that successful relational processing may require more general, attentional resources. If more attention must be paid to lower-level perceptual processes necessary for language comprehension, less attentional resources are available for the working memory operations especially critical for the processing of complex language structures.

While the processing of relations between items is crucial for successful language comprehension, at its heart language involves the processing of a different kind of relation -- the relation between language elements and real-world knowledge stored in long-term memory (see McKoon & Ratcliff, 1998). Words are symbols -- that is, they are associated with information that is not contained in the physical form of the word itself. It has been suggested that the human ability to remember, transform, and flexibly combine thousands of symbols is what especially sets us apart from other species (e.g., Deacon, 1997). Early in their processing, words are but perceptual objects whose visual or acoustic properties must be processed sufficiently to allow categorization and identification. Eventually, however, words serve as entry points into vast amounts of information stored in long-term memory. This associated information has been derived from many modalities (e.g., the shape and color of a carrot, its smell, its taste, its firmness and smoothness, the crunching sound made when eating it, etc.) and has come to be associated with the wordform through experience. The nature of the organization of long-term memory, the types of information that are stored, and the extent to which different information types are accessed under various conditions are all highly controversial issues.

Mirroring the concerns of psycholinguistics in general, many ERP investigations have been aimed at determining what kinds of information about words are typically retrieved during reading and listening and the time-courses with which this information is retrieved. Moreover, given its unique ability to track word, sentence, and discourse level processing with equal resolution, the ERP technique has also been directed at determining how information retrieved from the various words in a sentence is ultimately combined into a single message. ERP data suggest that the brain is clearly sensitive to some aspects of meaning by at least 250-300 milliseconds post-stimulus-onset. In this time window, the brain's response to words (and pronounceable pseudowords) in all modalities (spoken, printed, signed) (e.g., Holcomb & Neville, 1990; Kutas, 1987; Kutas & Hillyard, 1980a; Kutas & Hillyard, 1980b), to pictures (Ganis, Kutas, & Sereno, 1996; Nigam, Hoffman, & Simons, 1992) and faces (Barrett & Rugg, 1989; Bobes, Valdes-Sosa, & Olivares, 1994; Debruille, Pineda, & Renault, 1996), and to meaningful environmental sounds (Chao, Nielsen-Bohlman, & Knight, 1995; Van Petten & Rheinfelder, 1995) contains a negativity with a posterior, slightly right hemisphere distribution at the scalp.

Potentials at the same latency and sensitive to these same semantic variables are observed in the fusiform gyrus of patients with electrodes implanted for localizing seizure activity (e.g., McCarthy, Nobre, Bentin, & Spencer, 1995; Nobre & McCarthy, 1995; note that the polarity of a recorded potential depends upon the location of the active electrode and reference, such that the intracranially recorded "N400s" are not always negative). This so-called N400 component was mentioned previously in the discussion of frequency and repetition effects, as its amplitude varies with both. In children and intact adults, the N400 seems to be the normal response to stimuli that carry meaning -- or could, as in the case of pronounceable pseudowords. Some have suggested that the N400 reflects some kind of search through long-term, semantic memory; indeed N400 amplitude does vary with factors that also influence memory such as the number of items to be remembered (Stuss, Picton, & Cerri, 1986) and the length of the delay between presentations of an item (e.g., Chao et al., 1995). Its amplitude is diminished and its latency prolonged with normal aging, and even more so with various dementias (e.g., Iragui, Kutas, & Salmon, 1996; Iragui, Kutas, Mitchiner, & Hillyard, 1993).

We have suggested that the N400 indexes some aspect of meaning because its amplitude is modulated by semantic aspects of a preceding context, be it a single word, a sentence, or a multi-sentence discourse. For instance, the amplitude of the N400 to a word in a list is reduced if that word is preceded by one with a similar meaning (e.g., N400 amplitude to "dog" is reduced when preceded by "cat" compared to "cup", Brown & Hagoort, 1993; Holcomb & Neville, 1990; Van Petten, Reiman, & Senkfor, 1995). Brain activity in the same time region is also sensitive to phonological and orthographic relations between words (Barrett & Rugg, 1990; Polich, McCarthy, Wang, & Donchin, 1983; Praamstra, Meyer, & Levelt, 1994; Rugg, 1984a; Rugg, 1984b; Rugg & Barrett, 1987). Similarly, the amplitude of the N400 to a word in a sentence is reduced to the extent that the word is compatible with the ongoing semantic context. An anomaly (e.g., "He takes his coffee with cream and dog") elicits the largest N400 response. Nonanomalous, but less probable words (e.g., "He takes his coffee with cream and honey") generate less N400 activity than anomalies but of greater amplitude than more probable completions (e.g., "He takes his coffee with cream and sugar") (Kutas & Donchin, 1980; Kutas & Hillyard, 1980a; Kutas & Hillyard, 1980b; Kutas & Hillyard, 1984; Kutas, Lindamood, & Hillyard, 1984). Discourse level factors may also affect the magnitude of the N400 response. As single sentences, both "the mouse quickly went into its hole" and "the mouse slowly went into its hole" are congruous. However, in a larger discourse context (e.g., "Prowling under the kitchen table, the cat surprised a mouse eating crumbs. The mouse . . ."), the two adverbs (quickly and slowly) are no longer equally expected; in fact, the N400 response to "slowly" in this type of context is larger than the response to "quickly" (van Berkum, Hagoort, & Brown,

1999). Thus, at least around 400 milliseconds, lexical, sentential, and discourse factors seem to converge to influence language comprehension and do so in a fairly similar manner. When both lexical and sentential factors are present, they seem to influence the N400 amplitude independently (see also Fischler, Childers, Achariyapaopan, & Perry, 1985, for a similar conclusion; Kutas, 1993; Van Petten, 1993; Van Petten, 1995). The N400's relation to semantic integrative processes is further supported by the observation that its amplitude is greatly attenuated and its latency delayed in aphasic patients with moderate to severe comprehension problems but not in patients with equivalent amounts of damage to the right hemisphere (Swaab, Brown, & Hagoort, 1997).

The N400 is thus sensitive to the relationship between a word and its immediate sentential context and to that between a word and other words in the lexicon. Insofar as N400 indexes some aspect of search through memory, it seems then that the brain uses all the information it can as soon as it can to constrain its search. How does context serve to guide this search? We can think of information about word meaning as existing in a kind of space, structured by experience. The nature of this structure is often inferred from the outcome of various categorization or sentence verification tasks (e.g., Kounios, 1996; Kounios & Holcomb, 1992; Kounios, Montgomery, & Smith, 1994). Context (as well as the other factors known to influence N400 amplitude such as frequency or repetition) may serve to direct processing into different parts of this space -- usually parts that render subsequent searches easier by bringing the processor into a state "closer" to the meaning of the upcoming words. We have examined this hypothesis in a study where participants were asked to read pairs of sentences like:

Ann wanted to treat her foreign guests to an all-American dessert.

She went out in the back yard and picked some apples.

These sentence pairs were terminated with either the contextually expected item ("apples"), a contextually unexpected item that came from the same semantic category as the expected item (e.g., "oranges", another fruit), or an unexpected item from a different semantic category (e.g., "carrots"). Both types of unexpected endings elicited an N400 relative to congruent endings. However, even though both kinds of unexpected endings were equally inappropriate and implausible in the context, the unexpected item from the expected category elicited a smaller N400 than did the one from a different category. The extent of this reduction correlated with sentential constraint -- that is, how much the expected item was expected. These results suggest that the N400 is sensitive to the organization of background knowledge (the fact that apples and oranges share more features in common than apples and carrots) as well as to the relationship between

words and sentence contexts. More generally, the findings support the idea that on-line comprehension processes are influenced by the structure of background knowledge in long-term memory (for more details, see Federmeier & Kutas, 1999).

An integral part of language comprehension, therefore, involves retrieving from long-term memory world knowledge associated with particular words and groups of words. Context serves to shape both the nature of the information retrieved and the ease with which it can be found. Conceptual information also serves to shape language processing by providing a structure ("frame" or "schema") within which details beyond the level of individual words can be fit and related to one another. These "schemas" can be thought of as the brain's general expectations about the nature of information that will be retrieved and the order in which it will come. These schemas might well influence the extent to which information is attended, how it is stored into working memory, and the ease with which it is comprehended. In a recent study, Munte, Schiltz, and Kutas (1998b) examined how people's schemas about time (built of daily experience) may affect the brain's processing of sentences and interact with working memory variables. People read sentences describing the temporal order of two events; they differed only in whether their initial word was "before" or "after" (e.g., "Before/after the students took the exam the teacher called the parents"). While these sentence types are otherwise identical in lexical content and syntactic structure, they differ in the extent to which they fit with our schema of time as a dimension moving from past to future. In "after" sentences, the two events are mentioned in accordance with this conception -- the temporally earlier event coming first and the temporally later event coming second. By contrast, "before" sentences reverse this natural order. Munte et al. found that starting within 300 milliseconds of the initial word (the temporal term), "after" sentences showed a larger sustained positivity than did "before" sentences; this positivity was similar to that described for the relative clause (object vs subject) contrast. This difference was, again, most pronounced for individuals with high working memory spans. The data suggest that our knowledge of the world (in this case, about time) has an immediate, lasting effect on processing, and their impact is modulated by working memory capacity and/or availability. Words like "before" and "after" serve as cues about the relationship between elements to come. These relations, in turn, are easier to process if they conform to general conceptual patterns derived from experience.

3. Language production, or the time it takes to name a picture

Language comprehension is only half the picture of "language processing". We not only hear and read but also speak and write. Indeed, these two in combination

unarguably distinguish the human from the non-human primate (even the ones that can communicate via sign language). Until recently, however, language production has been little explored electrophysiologically. The act of speaking generates many electrical artifacts (due to e.g., tongue, face, and dental fillings), making it difficult to extract just the brain events of interest. There are, however, two ERP methods for examining motor preparation -- even for actions that are never actually performed (e.g., words that are never uttered). Using these, investigators have begun to ask when certain types of information become available to influence the motor planning and preparation that is at the heart of language production.

One such method is based on the Lateralized Readiness Potential (LRP). The LRP is derived from the "readiness potential" (RP), a negative-going potential that develops (primarily over central sites) about a second or so before a voluntary hand movement. Approximately half a second before the actual movement, the RP becomes lateralized, with larger amplitudes over the hemisphere contralateral to the moving hand (e.g., Kutas & Donchin, 1974). By averaging the lateralization for movements made with the left and right hand, lateralized activity that is not related to motor preparation cancels out; the remaining LRP reflects the average amount of lateralization specifically related to motor preparation.

To investigate language production using the LRP, Van Turennout, Hagoort, and Brown. (1997) asked individuals to name pictures of objects and animals aloud. On half of the trials, a cue signaled participants to postpone their naming response and to perform a go/no-go task. The instruction was, for example, to press the right button if the picture was of an animal and the left if it was of a vegetable; however, the response was to be given only if the name of the picture ended with an "r" and not if it ended with an "s" (all pictures' names ended in either "r" or "s"). If conceptual (semantic) information about the picture is available prior to phonological information, one might assume that participants would prepare the correct responding hand before they are able to determine whether or not they should actually make a response. This is, in fact, the pattern that Van Turennout et al. observed: the brain began motor preparation of the appropriate hand based on semantic information that was, apparently, available first, and so the LRPs to both go and no-go trials look initially similar. Only later did phonological information become available to inhibit the response in the no-go case. A similar, later experiment found that syntactic information also becomes available before phonological information (Van Turennout, Hagoort, & Brown, 1998).

When individuals are asked to respond to one class of stimuli (go trials) but not to another (nogo trials), the ERP to the nogo trials is characterized by a large frontally distributed negativity (N200) that seems to be a function of neural activity required for response inhibition. By changing the information on which a go/no-go decision is reached, the

peak latency of the N200 effect can be used to examine when certain types of information are available to the part of the system responsible for response inhibition. Using a go/no-go picture processing task with German speaking participants, Schmitt, Munte, and Kutas (2000) examined N200 latencies to no-go decisions based on semantic (animal vs. object) and phonological information. They found that the information needed to execute response inhibition was available about 90 milliseconds earlier when it was based on the semantic information as compared with the phonological information. Together, Van Turenout et al. and Schmitt et al.'s results suggest that different types of information become available to the language production (or at least the motor) system at varying times, from semantic/conceptual to syntactic to phonological. As with other cognitive domains, models of information processing for language production are better served by designs that track the brain's activities both prior to and following overt behaviors.

4. Conclusions

Comprehending and producing language thus involves a number of different kinds of brain processes including perceptual analysis, attention allocation, retrieval of information from long-term memory, storage of information into working memory, and comparisons between/transformations of information contained in working memory. These processes take place at multiple levels for different types of information (orthographic/phonological word form information, morphological/syntactic information, conceptual/semantic information) and unfold with different time courses; they are thus reflected in different electrophysiological processes with different time-courses.

Understanding language processing, therefore, requires understanding how the multiple subprocesses involved interact over time and space. This, in turn, requires an understanding of how the brain's processing of language interacts with more general processing demands. For example, both N400 and P600 amplitudes are sensitive to attentional manipulations. The N400 is not observed when the priming context is masked (Brown & Hagoort, 1993), and N400 effects in word pair tasks are larger when the prime target interval is short and the proportion of related word pairs is high (Chwilla, Brown, & Hagoort, 1995; Holcomb, 1988). Similarly, the P600 to verb inflection errors is greatly attenuated if not absent when people are asked to scan sentences merely to determine whether a word in a sentence is printed in upper case (Gunter & Friederici, 1999). Orthographic, phonological, morphological, syntactic, and pragmatic priming and context ERP effects seem to overlap temporally between 200-400 msec, and this is also an interval in which various

memory-related and some attention-related ERP effects are observed. Moreover, the transient ERPs to analyzing a visual stimulus as a word (including discrimination, categorization, and violation detection) are superimposed on the slower potentials that seem to be elicited during the processing of sentences and various tasks requiring that information be retrieved from longer term memory. Indeed, it remains to date unknown the extent to which any of these processes or ERP effects are specific to language.

What we do know is that language processing is a complex skill involving the whole brain. The goal of electrophysiological investigations of language, as well as the goal of research exploring language processing with other tools, is to build an understanding of how the various processes involved in language comprehension and production are coordinated to yield the message-level understanding we gain from reading or listening to speech, on the one hand, or to allow us to get a word in edgewise, on the other.

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