

CHAPTER ONE

TIME FOR MEANING: ELECTROPHYSIOLOGY PROVIDES INSIGHTS INTO THE DYNAMICS OF REPRESENTATION AND PROCESSING IN SEMANTIC MEMORY

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Contents


1. Introduction	2
2. Conceptual Structure and Neural Structure	3
2.1. Modality-Independent Semantics	4
2.2. Modality- and Category-Dependent Semantics	6
2.3. Distributed Semantics and the “Binding Problem”	7
3. Electrophysiology and the N400	9
3.1. The N400 Component	10
3.2. Neural Loci of the N400	12
3.3. The N400 and Conceptual Structure and Flexibility	15
3.4. The N400: A Neural Marker of Processing in Semantic Memory	17
4. From Input to Meaning	17
4.1. Models of Visual Word Recognition	18
4.2. Constraints on the Mapping of Inputs to Semantics?	20
4.3. Meaning in Context	23
5. Semantics “ON TIME”	27
5.1. How When Determines What	29
5.2. Semantics Beyond the N400	32
6. Conclusions	34
References	34

Abstract

At least since the time of Aristotle, humans have been fascinated with trying to understand how meaning is represented in what, in modern terms, has come to be known as semantic memory. Behavioral science, computational modeling, neuropsychology, hemodynamic imaging, and electrophysiological techniques have all been applied to the task of delineating how semantic memory is instantiated in the brain. As reviewed in this chapter, the collective data from

1 these methods are providing an increasingly detailed picture of the functional 1
2 and neural organization of semantic memory. What remains less clear are the 2
3 dynamics of how meaning is accessed and used. Those dynamics, however, are 3
4 beginning to be revealed by data from temporally sensitive measures, such as 4
5 electrophysiology. In particular, studies of the N400 event-related potential 5
6 (ERP) component suggest that considerations of time may hold the key to 6
7 understanding how information represented in disparate areas of the brain 7
8 comes to be bound in the structured-yet-flexible manner that is the hallmark 8
9 of human semantic processing. 9
10

11 **1. INTRODUCTION** 11

12  12
13 13
14 Imagine walking into a library and finding books, periodicals, and 14
15 maps shelved and stacked in a haphazard, nearly random fashion—a cluster 15
16 of books of the same color, a shelf of large books, a pile of recently used 16
17 periodicals. The usefulness of such a library would be quite limited because, 17
18 although it might contain a great deal of information, that information 18
19 would be nearly impossible to find in any reasonable amount of time. 19
20 In fact, this was the state of most libraries in the United States prior to 20
21 1876 when Melvil Dewey first published his now widely used system of 21
22 library organization, the Dewey Decimal system. This classification system 22
23 and the others that followed it are arguably the cornerstone of libraries and 23
24 other information reservoirs because such systems transform information 24
25 warehouses into information databases. 25

26 Like libraries, human brains are storehouses of vast amounts of different 26
27 kinds of information. In what is typically referred to as semantic memory, 27
28 the human brain stores information about objects, including what they 28
29 look, sound, feel, smell, and taste like, how they move, and how they are 29
30 used, and about places, actions, and events. Information about the faces, 30
31 voices, and biographies of people in the movies and in the neighborhood is 31
32 also maintained, as is information about words, including their spelling, 32
33 sound, and meaning, and the patterns in which they cooccur. And, like 33
34 libraries, human brains must not only store all of this information but also 34
35 make it available for use, in varied contexts and often in only a few hundred 35
36 milliseconds or less. The question of how information is represented in and 36
37 accessed from semantic memory is therefore a central one for both psychol- 37
38 ogy and neuroscience. It has implications for how knowledge is acquired 38
39 and lost (with age, disease, or trauma), what kinds of information will 39
40 become available in response to a particular stimulus, and when and how 40
41 knowledge will be used in a particular task situation (i.e., what inferences 41
42 and what errors are likely to be made). Indeed, the study of semantic 42
43 memory is arguably the study of the filter through which the human 43
44 being views and interacts with her world. 44

1 The organization and dynamics of semantic memory have been studied 1
2 with a wide variety of perspectives and techniques. As will be reviewed in 2
3 the first part of this chapter, neuropsychological and hemodynamic imaging 3
4 studies have converged to provide a picture of how meaning-related infor- 4
5 mation is organized in the brain and where it is stored. In particular, it is 5
6 becoming increasingly clear that meaning is represented in a highly 6
7 distributed fashion and that multiple brain areas are involved in semantic 7
8 access and processing. This emerging understanding of semantic represen- 8
9 tation in the brain, however, emphasizes the critical “binding problem,” 9
10 which asks how distributed feature information is brought together to create 10
11 the integrated concepts that humans experience, remember, and use to 11
12 communicate and reason. The second part of the chapter, therefore, discusses 12
13 how considerations of time, and data provided by temporally precise 13
14 measures such as event-related brain potentials, can speak to the dynamics 14
15 of semantic access and thereby enrich the understanding of how the brain 15
16 represents and processes meaning. 16

2. CONCEPTUAL STRUCTURE AND NEURAL STRUCTURE

21
22
23 Words signify substance, quality, relation, place, position, state, action or 23
24 affection . . . roughly, examples of substance are ‘man’ or ‘horse’, of quantity 24
25 such terms as ‘two cubits long’ or ‘three cubits long’, of quality such 25
26 attributes as ‘white’, ‘grammatical’ . . . 26

Aristotle (350 B.C.E.), *The Categories* 27

28 Concepts are mental representations of a type or class, often including a 28
29 great deal of multifaceted information. For example, the concept of dog is 29
30 likely to include information about its typical shape and size, the feel of its fur, 30
31 and the sound of its bark, as well as more abstract information such as what it is 31
32 likely to eat, how it behaves, its usual lifespan, and so forth. The idea that 32
33 concepts may be grouped into categories, which are organized by similarity and 33
34 structured into taxonomies, has a longstanding tradition in western philosophy 34
35 (e.g., Aristotle, 2006; Kant, 1996), and continues to be a prominent view in 35
36 cognitive psychology (see review and critiques in Murphy, 2002). Approaches 36
37 to understanding semantic memory that utilize techniques from neuropsy- 37
38 chology and cognitive neuroscience have generally assumed that this concep- 38
39 tual information resides in a specialized semantic system, which is accessed via 39
40 connections between unimodal, perceptual areas (e.g., the left fusiform gyrus 40
41 in the case of visual orthographic input or the primary and secondary auditory 41
42 cortices in the case of acoustic input) and “association areas” (especially the left 42
43 inferior prefrontal cortex and perisylvian cortex) that process information 43
44 originating from multiple sensory modalities. 44

1 Within this framework, two distinct kinds of questions have been asked. 1
2 The first arises out of traditional cognitive theories of semantic memory, 2
3 which posit that conceptual information resides in a semantic store, where it 3
4 is represented in an “amodal” format (i.e., a format that does not make 4
5 reference to the physical form by which that information was originally 5
6 delivered; Pylyshyn, 1980). Studies in this line of work have therefore 6
7 sought to delineate the brain areas that are involved in processing for 7
8 meaning that occurs regardless of input modality (e.g., auditory words, 8
9 visual words, pictures) or type (e.g., action verb, concrete noun). Research 9
10 examining this question often adopts the approach, which reaches back to 10
11 PET studies in the late 1980s and early 1990s (e.g., Petersen & Fiez, 1993; 11
12 Petersen, Fox, Posner, Mintun & Raichle, 1989), of using multiple sub- 12
13 tractions to try to isolate areas selectively involved in semantic processing. 13
14 A core assumption of this approach is that areas that participate in amodal 14
15 semantic processing should be more active during semantic tasks than 15
16 during, for example, phonological, orthographic, or complex perceptual 16
17 tasks performed on the same items. They should also be more active when 17
18 processing words than when processing various types of equally perceptually 18
19 complex, but meaningless, controls such as pseudowords, illegal strings of 19
20 letters or combinations of sounds, or visual or auditory noise. 20

21 The second question typically addressed by cognitive neuroimaging and 21
22 neuropsychological studies of semantic organization is essentially the inverse 22
23 of the first: what brain areas are involved in semantic processing but are not 23
24 independent of input modality or category? For example, are there separable 24
25 areas involved in processing auditory and visual words for meaning (e.g., 25
26 Marinkovic et al., 2003)? Do different cortical areas subserve the representa- 26
27 tion of living and nonliving entities (e.g., Leube, Erb, Grodd, Bartels, & 27
28 Kircher, 2001; Thompson-Schill, Aguirre, D’Esposito, & Farah, 1999) or 28
29 other types of categories? This second question builds on initial findings in 29
30 neuropsychology suggesting that focal brain lesions can result in the 30
31 impairment of semantic knowledge about particular semantic categories 31
32 (e.g., living vs. nonliving things, abstract vs. concrete words; Warrington & 32
33 Shallice, 1984). As will be discussed in more detail, growing evidence that 33
34 semantic information may be distributed across a large number of brain areas, 34
35 many of which are clearly modality specific, raises the important question of 35
36 how integrated conceptual entities come to be built from distributed repre- 36
37 sentations of semantic features (e.g., how the features {furry}, {barking}, and 37
38 {loyal} become experienced as the concept “DOG”). 38

39 40 2.1. Modality-Independent Semantics 40 41

42 When PET and (later) fMRI methodologies became widely available in the 42
43 late 1980s and early 1990s, one primary goal of cognitive neuroscientists 43
44 interested in semantic memory was identifying amodal semantic processing 44

1 areas. That is to say, cognitive neuroscientists began by trying to find areas 1
2 that could be associated with the semantics “box” in cognitive box and line 2
3 models, such as the “Content System” box and “Semantic Attributes” line 3
4 in the classic Logogen model (Morton, 1969), the (unimplemented) 4
5 “Meaning” ellipse in the influential Parallel-Distributed Processing (PDP) 5
6 model (Seidenberg & McClelland, 1989), or the (again, unimplemented) 6
7 “Semantic System” box in the Dual-Route Cascaded (DRC) model of 7
8 word reading (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001). Hemo- 8
9 dynamic imaging methods, which spatially localize neural activity by track- 9
10 ing accompanying changes in blood flow and blood oxygenation levels, 10
11 offered the promise of being a window on semantics “in action,” thereby 11
12 allowing a determination of which brain areas are ubiquitously involved in 12
13 the processing of meaning in the normally functioning human brain. 13

14 One of the first PET studies of word processing (Petersen, Fox, Posner, 14
15 Mintun, & Raichle, 1988) began in this vein by contrasting activations in 15
16 response to a semantic generation task to those in response to speaking 16
17 words aloud. Importantly, both the semantic generation task and the 17
18 speaking task were performed with cue words presented in both the visual 18
19 and auditory modalities, so that regions more active in the semantic task 19
20 regardless of presentation modality could be identified. The left inferior 20
21 prefrontal cortex and the anterior cingulate cortex (especially the inferior 21
22 anterior cingulate), both met the joint criteria of being more active in the 22
23 semantic task than in the reading aloud task and of being active when task 23
24 cues were presented in both the auditory and visual modality. 24

25 Many PET and fMRI studies that followed this original, ground-breaking 25
26 one eventually came to a consensus that a broad network of areas, including 26
27 the left inferior prefrontal cortex, the posterior temporal cortex, and more 27
28 anterior regions of the temporal lobe are all involved in semantic processing 28
29 (e.g., Demonet et al., 1992; Petersen et al., 1989; Pugh et al., 1996; 29
30 Shaywitz et al., 1995), even in the absence of an explicit semantic task 30
31 (i.e., during the incidental semantic processing that occurs while performing 31
32 any task with orthographic stimuli; Price, Wise, & Frackowiak, 1996). This 32
33 proposed network, derived from the study of normal adults, roughly corre- 33
34 sponds to areas that had already been identified as critical to semantic 34
35 processing based on patient studies dating back to the 1800s (Dejerine, 35
36 1892; Geschwind, 1967; Whitehouse, Caramazza, & Zurif, 1978). 36
37 The correspondence between the two approaches is not expected to be 37
38 perfect, as neuroimaging identifies brain areas that are *involved in* the proces- 38
39 sing of meaning whereas neuropsychology picks out in particular those that 39
40 are most *necessary for* normal semantic functioning. However, taken 40
41 together, neuropsychological and neuroimaging data suggest that semantic 41
42 processing depends, at least in part, on the involvement of frontal and 42
43 temporal lobe areas that are able to process information from multiple 43
44 sensory modalities. 44

2.2. Modality- and Category-Dependent Semantics

In addition to identifying areas involved in the general, modality-independent processing of meaning-related information, neuroimaging studies have sought converging evidence for the kind of category-dependent processing deficits that have sometimes been implicated in studies of lesion patients. These include distinctions between the areas involved in the semantic processing of living things versus inanimate objects (Warrington & Shallice, 1984), tools versus other types of objects (Warrington & McCarthy, 1987), content versus function words (Benson, 1979; Caramazza & Berndt, 1985), nouns versus verbs (Damasio & Tranel, 1993), and concrete versus abstract words (Warrington, 1981).

Like neuropsychological studies, neuroimaging studies have identified patterns of activation that differ for different types of meaningful inputs, although these patterns are not always consistent across studies and their significance has been disputed (Devlin et al., 2002; Thompson-Schill et al., 1999). In at least some cases, brain areas associated with particular types of processing deficits in patients have also been found to show modality- or category-dependent patterns of activation in neuroimaging studies. For example, a study explicitly comparing lesion locations for patients impaired in the naming of people, animals, and tools to PET activations observed in brain-intact adults naming the same objects found a number of correspondences (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996). Overlapping areas in the anterior temporal cortex were associated with the naming of people, whereas more posterior temporal regions were associated in both groups with naming animals. Similarly, the lesions causing deficits to naming tools were also in the areas active while healthy participants named tools in the scanner. The study can also be taken as support for a more general distinction between the areas involved in processing living and nonliving things, as the activations observed in response to naming living things (people, animals) were always more anterior than those in response to naming nonliving things (tools).

Another example of correspondence between neuropsychology and neuroimaging comes from a PET study that examined the areas active in normal adults during the generation of colors or actions associated with an object (e.g., the color “red” or the action “drive” in association with an achromatic drawing of a stop sign; Martin, Haxby, Lalonde, & Wiggs, 1995). Left-lateralized fusiform gyrus activity was observed in response to the generation of color but not action words, in accordance with neuropsychological studies indicating that color blindness can be the result of fusiform gyrus damage (Zeki, 1990). Generation of action but not color words involved activity in the left inferior frontal lobe, in accordance with neuropsychological studies indicating that left frontotemporal damage can result in an impairment of verb processing (e.g., Caramazza & Hillis, 1991).

1 The identification of brain areas that seem to be involved in meaning 1
2 processing only for particular types of input raises several questions. First, 2
3 why should any such areas exist at all, rather than all semantic processing 3
4 being accomplished by amodal processing areas, as many psychological 4
5 models have assumed? Second, why are dissociations observed for some 5
6 distinctions (e.g., living versus nonliving things) but not others (e.g., round 6
7 objects versus triangular ones, or red objects as opposed to yellow ones)? 7
8 Finally, one might ask what principles underlie the observed neural pattern— 8
9 that is, for example, why are posterior temporal areas but not inferior frontal 9
10 ones involved in the processing of tools? An appealing theory for addressing 10
11 these questions is that the organization of conceptual information in the 11
12 brain is driven by the perceptual and motor areas that become active during 12
13 the encoding of that concept's meaning (e.g., Barsalou, Simmons, Barbey, & 13
14 Wilson, 2003; Damasio, 1989; Pulvermuller, 1999; Shallice, 1988). 14

15 For example, under the Hebbian theory proposed by Pulvermüller 15
16 (1999), the neural representation of a word has two parts: the form part, 16
17 localized to classical language areas in the left perisylvian cortex and repre- 17
18 senting information such as the pronunciation of the word, and the concep- 18
19 tual part, localized to brain areas that were active during the encoding of 19
20 the associated form part's semantics. This account provides an explanation 20
21 of both why modality- and input-type-dependent semantic processing areas 21
22 exist and also why they exist in the particular areas to which they have been 22
23 localized (and not others). For example, according to this type of theory, the 23
24 semantic representation of words that are learned primarily by co-occurrence 24
25 of a particular phonological or orthographic form with a particular class of 25
26 visual inputs will include high level visual cortices, because high level visual 26
27 cortices become active coincidentally with the verbal label (e.g., if SL points 27
28 at her dog and says to KDF's young daughter "Shih-tzu," KDF's daughter 28
29 will process the visual form of the shih-tzu coincidentally with hearing 29
30 "Shih-tzu."). Similarly, the semantic representation of action verbs might 30
31 involve motor cortices because learning what the word "jump" means often 31
32 involves seeing or imagining others jump, or jumping oneself. Explanations of 32
33 this type have been put forward for all of the category-based distinctions 33
34 described thus far (see Pulvermuller, 1999, for an extensive discussion), 34
35 although arguments against this view have also been levied (e.g., Caramazza 35
36 & Mahon, 2003; Caramazza & Shelton, 1998, 1999). 36

37 38 **2.3. Distributed Semantics and the "Binding Problem"** 38 39

40 Theories that explain the organization of conceptual information in the 40
41 brain via links between conceptual and sensory-motor processing differ in 41
42 whether they view sensory and motor areas as the actual locus of semantic 42
43 representations (the multiple semantic systems view of, e.g., Shallice, 1988) 43
44 or as participants in conceptual processing, which arises as an emergent 44

1 property of activity distributed across sensory–motor and association areas 1
2 (e.g., Damasio, 1989). Other views of how the functional subcomponents 2
3 of semantics are divided over brain areas have also been put forward, such 3
4 as the Organized Unitary Content Hypothesis (Caramazza, Hillis, Rapp, & 4
5 Romani, 1990) or the Conceptual Structure Account (Taylor, Moss, & 5
6 Tyler, 2007). Despite important differences across these views, a critical 6
7 similarity is that all acknowledge that semantic processing engages a sizeable 7
8 network of neural areas, including the left inferior prefrontal cortex, ante- 8
9 rior and posterior temporal lobes, and tempo-parietal areas (Price, 2000; 9
10 for reviews, see Martin, 2007; Thompson-Schill, 2003). As will be the focus 10
11 of the remainder of the chapter, it seems critical to understand how infor- 11
12 mation in this neurally and (under most accounts) functionally distributed 12
13 system comes to be reliably integrated to yield the subjective experience of 13
14 unified concepts (associated with particular verbal labels) and how the 14
15 organization of featural information in subsystems or subparts of the system 15
16 ultimately yields conceptual-level organization. 16

17 This “binding problem” is a particularly difficult one because the human 17
18 conceptual system displays a remarkable combination of both stability and 18
19 flexibility. Experienced language users are able to rapidly and consistently 19
20 map tens of thousands of arbitrary word forms (from multiple modalities, in 20
21 the case of literate language users) onto concepts. Yet, the exact configura- 21
22 tion of conceptual features accessed for a given word—even an unambigu- 22
23 ous one, let alone a homographic or homophonous one—seems to be 23
24 highly affected by context. For example, although a “moving” context 24
25 might highlight the weight of a piano and tend to emphasize its similarity 25
26 to other types of furniture, a “symphony” context might highlight the 26
27 function of a piano and thus tend to emphasize its similarity to other types 27
28 of musical instruments (e.g., Barclay, Bransford, Franks, McCarrel, & 28
29 Nitsch, 1974; Tabossi & Johnson-Laird, 1980). Along the same lines, 29
30 although across cultures, individuals, and time there is a considerable degree 30
31 of consistency in the concepts that are considered to be “good” representa- 31
32 tives of their categories (so-called “typicality effects” as described by Rosch 32
33 (1973) and Rips, Shoben, and Smith (1973)), these similarity structures can 33
34 also be readily altered by context. For example, while out of context 34
35 “robin” is considered a more typical bird than “chicken,” after reading a 35
36 sentence like “The bird walked across the barnyard,” the word “chicken” is 36
37 rated as more typical (and responded to more quickly) than is “robin” 37
38 (Roth & Shoben, 1983). 38

39 Finally, while many conceptual categories seem to have a nearly univer- 39
40 sal existence and structure (as predicted by theories that attribute the driving 40
41 principles for category structure to the organization of the human brain), it 41
42 is also the case that people are quite proficient at creating novel (*ad hoc*) 42
43 categories to meet particular goals—for instance, “things to pack in a small 43
44 suitcase on a trip to London” (Barsalou, 1983). Thus, even as there seems to 44

1 be reproducible structure to categories, there also seems to be flexibility and
2 variability in the details of these structures over contexts, experiences, and
3 individuals. This makes it unlikely that integration in the distributed seman-
4 tic system is accomplished in a hard-wired fashion. Instead, what is needed is
5 a means of linking spatially distributed information together in a manner
6 that can be both reliable and stable, but also flexible. That critical ingredient
7 may be time.

3. ELECTROPHYSIOLOGY AND THE N400

14 Whereas imaging techniques that track blood flow or blood oxygena-
15 tion levels, such as PET or fMRI, can provide reliable information about
16 the spatial location of neural activity, they afford relatively poor information
17 about the timing of that activity, in part because such hemodynamic
18 changes simply do not track neural activity on a millisecond level. Informa-
19 tion about timing can be obtained, instead, from techniques that directly
20 measure neural electrical activity. Neural communication takes place via
21 current flow that generates an electrical potential in the conductive media
22 inside and outside of neurons. The electrical potentials of a large number of
23 these neurons that are arranged in a systematic fashion and activated in
24 synchrony—conditions that seem to hold for cortical pyramidal cells,
25 among others—will summate to create a signal large enough to be measured
26 with electrodes placed on the scalp (e.g., Kutas & Dale, 1997). The contin-
27 uous, rhythmic electrical activity of the brain as measured from the scalp
28 is known as the electroencephalogram or EEG. Embedded within this
29 signal are small, transient voltage fluctuations associated with perceptual,
30 emotional, cognitive, and response-related processing elicited by specific
31 events, such as the impingement of a stimulus on the sensory receptors.

32 To capture the brain activity associated with events of interest, where an
33 “event” is broadly defined and could reflect, for example, even the absence of
34 an expected stimulus, event-related potentials (ERPs) can be derived by
35 extracting portions of the EEG activity that are time-locked to those
36 events—often, stimulus onset or a behavioral or motor response. A number
37 of these extracted segments are averaged together so that temporally specific
38 activity (signal) can be distinguished from temporally nonspecific activity
39 (noise). The resulting waveforms, one for each recording channel and each
40 condition of interest, reflect voltage fluctuations over time either following
41 or, in some cases, preceding the triggering event. Changes in the timing,
42 amplitude, and scalp distribution of the ERP as a function of experimental
43 manipulations can then be used to make inferences about neural and cogni-
44 tive aspects of processing (e.g., Munte, Urbach, Duzel, & Kutas, 2000).

3.1. The N400 Component

A particular part of the ERP signal, sometimes called a “component” of the ERP, has been specifically associated with the processing of semantic information. The N400—so-called because it is a negative-going voltage fluctuation that tends to peak around 400 ms after stimulus-onset—was first observed in response to words that were semantically anomalous in their sentence contexts (e.g., “He spread the warm bread with socks”; Kutas & Hillyard, 1980b). Kutas and Hillyard anticipated that these anomalous words would elicit a P300, a positive-going ERP component that had been broadly linked to the processing of unexpected events of a wide variety of types (e.g., Duncan-Johnson & Donchin, 1977; Ruchkin, Sutton, & Tueting, 1975). Instead, they observed a larger negativity to the semantically unexpected, as compared with the expected, sentence endings. Figure 1 shows an example. However, words that were unexpected for other reasons—for example, because they appeared in an unexpected size—did elicit the anticipated P300 response (Kutas & Hillyard, 1980a). This was thus the first hint that the brain treats manipulations that impact meaning differently from those that do not.

Subsequent research has established that the N400 is not actually a marker for semantic unexpectedness as such. Instead, the N400 seems to

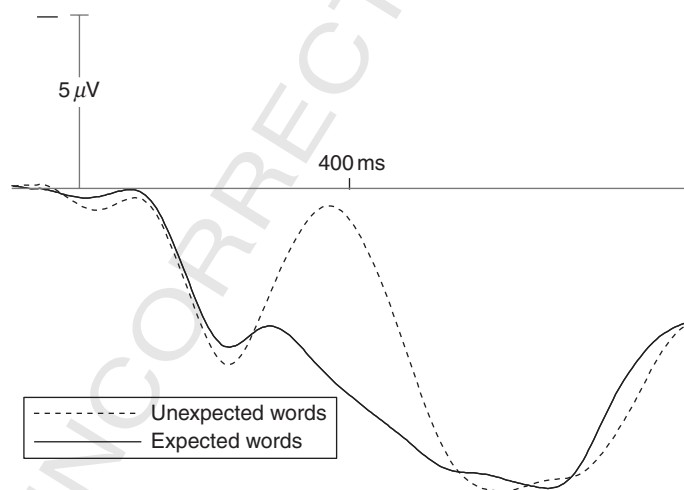


Figure 1 N400 sentential congruency effect. N400 responses are reduced in amplitude for words that are expected in a sentence context relative to those that are not. Thus, for example, the word “dog” elicits smaller mean amplitude responses between 250 and 500 ms poststimulus onset than does the word “sugar” as a completion for the sentence context “I take my coffee with cream and . . .” In this and all subsequent figures, responses are shown at a middle, centro-posterior channel, with negative voltage plotted up.

1 be part of the normal response to potentially meaningful stimuli. In some 1
2 respects, the N400 resembles the “sensory” ERP components that generally 2
3 precede it in time. These components are obligatorily elicited by the 3
4 apprehension of a stimulus in a particular modality (a different pattern of 4
5 sensory components characterizes the response to stimuli in each modality; 5
6 for a review, see Munte et al., 2000), and their characteristics (amplitude, 6
7 latency, and distribution) are largely controlled by the physical properties of 7
8 that eliciting event. The elicitation of the N400 seems similarly obligatory, 8
9 but less yoked to sensory processing, as N400s are observed to meaningful 9
10 stimuli across modality. In other respects, the N400 is also similar to more 10
11 “cognitive” components, which generally occur later in time and are fairly 11
12 modality-independent. Cognitive components are highly affected by the 12
13 information processing demands placed upon the person by the task envi- 13
14 ronment. Thus, in different task environments, the same stimulus may elicit 14
15 a very different response pattern on these components, and, indeed, such 15
16 components can even be elicited in the absence of an external triggering 16
17 event, if that absence is informative (e.g., Ruchkin et al., 1975). The N400 17
18 shares at least one characteristic with this type of component, in that it is 18
19 strongly affected by the contextual setting of an eliciting stimulus (e.g., the 19
20 same word presented in a list or as a sentence completion can elicit very 20
21 different N400s). 21

22 N400s are thus an interesting blend of ERP component “types.” As will 22
23 be discussed in more detail, N400s are elicited and modulated by stimuli of 23
24 a wide variety of types in all modalities. However, not all stimuli elicit clear 24
25 N400 activity; those that do tend to be associated with meaning, such as 25
26 words and pictures (e.g., Ganis, Kutas, & Sereno, 1996; Kutas, Neville, & 26
27 Holcomb, 1987). Such stimuli elicit N400s even when they are processed 27
28 incidentally and/or with little conscious awareness, as during some stages of 28
29 sleep (Brualla, Romero, Serrano, & Valdizan, 1998), with masking 29
30 (Deacon, Hewitt, Yang, & Nagata, 2000; Kiefer, 2002; Misra & 30
31 Holcomb, 2003), or during the attentional blink (Rolke, Heil, Streb, & 31
32 Hennighausen, 2001; Vogel, Luck, & Shapiro, 1998). The amplitude (but 32
33 not the latency) of the N400 to these stimuli is modulated, not by the kind 33
34 of perceptual parameters that tend to affect sensory components, but by 34
35 factors specifically related to the ease of semantic processing for these stimuli 35
36 (for a review, see Kutas & Federmeier, 2000). Manipulations of physical and 36
37 linguistic variables that do not affect meaning (such as grammatical errors; 37
38 Kutas & Hillyard, 1983) do not modulate the N400, and N400 effects are 38
39 also not seen to unexpected events in other structured domains, such as 39
40 music (e.g., Besson, Faieta, Peretz, Bonnel, & Requin, 1998). Thus, the 40
41 N400 seems to be functionally specific to the processing of meaning, and, as 41
42 described next, a large body of research points to the N400 as an electro- 42
43 physiological marker of processing in the distributed semantic memory 43
44 system. 44

3.2. Neural Loci of the N400

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If the N400 reflects processing in semantic memory, then its neural origins would be expected to line up with the brain areas highlighted by functional imaging and neuropsychological studies. The N400 has a wide scalp distribution; it can be seen at most scalp sites, although it tends to be largest over the center of the head. This pattern would tend to implicate a distributed source, and, in fact, attempts to model the electrophysiological data have pointed to a wide-spread collection of cortical sources (Haan, Streb, Bien, & Rosler, 2000). However, the inverse problem—that is, attempting to determine the neural sources responsible for a particular scalp pattern—is mathematically ill-defined and is particularly difficult to solve for multifaceted, diffuse sources, as the N400 seems to be. Therefore, researchers have turned to other techniques, such as the use of intracranial recordings, which measure electrophysiological signals from electrodes placed on the surface of the cortex or implanted within it, or the measurement of the magnetoencephalogram (MEG) or the event-related optical signal (EROS), which each also track correlates of brain electrical activity with high temporal resolution but provide better spatial sampling.

A number of MEG studies (e.g., Halgren et al., 2002; Helenius & Salmelin, 2002; Helenius, Salmelin, Service, & Connolly, 1998, 1999; Kwon et al., 2005; Pylkkanen & McElree, 2007; Simos, Basile, & Papanicolaou, 1997; Uusvuori, Parviainen, Inkinen, & Salmelin, 2008) and one EROS study (Tse et al., 2007) have attempted to localize the activity responsible for the N400. These studies have fairly consistently pointed to sources in the superior/middle temporal gyrus, the temporoparietal junction, and the medial temporal lobe. Dorsolateral frontal cortical regions have also been implicated in some studies (Helenius et al., 1998). Although several of these studies have recorded only over the left hemisphere, studies that have recorded activity from both hemispheres have tended to find bilateral activity (consistent with growing data pointing to an important role for the right hemisphere in meaning processing; see, e.g., the review by Federmeier, Wlotko, and Meyer, (2008)), although the right hemisphere source is often found to be weaker. Thus the same network of brain areas that have been implicated in amodal semantic processing by imaging studies seem to be an important part of the source of scalp-recorded N400 activity.

MEG and EROS studies can provide information not only about the source of brain electrical activity associated with semantic processing, but also its timecourse. Halgren et al.'s (2002) data, for example, suggest that the scalp-recorded N400 reflects a wave of activity beginning around 250 ms poststimulus-onset in the posterior half of the left superior temporal gyrus, spreading forward and ventrally to encompass most of the left temporal lobe by 365 ms, and then spreading to the anterior temporal lobe in the right

1 hemisphere and to the frontal lobe bilaterally by the peak of the N400 1
2 response (between 370 and 500 ms). The only EROS N400 study 2
3 (Tse et al., 2007) found a similar progression of activity from the superior 3
4 temporal lobe to frontal areas and then back again. These findings are 4
5 complemented by work using intracranial recordings, typically from 5
6 patients undergoing preoperative evaluation for epilepsy surgery. Whereas 6
7 deep cortical sources may be difficult to see with EROS and MEG (because 7
8 of various physical limitations on the signal strength), intracranial data in 8
9 N400-eliciting paradigms have typically been collected from the medial and 9
10 inferior temporal lobe (where epileptic sources are most frequent). Intra- 10
11 cranial studies have identified a source in the anterior medial temporal lobe 11
12 that patterns closely with the scalp-recorded N400 in its sensitivity to 12
13 semantic priming, semantic anomaly, repetition, and verbal memory 13
14 (Elger et al., 1997; Fernandez et al., 2001; Guillem, N'Kaoua, Rougier, & 14
15 Claverie, 1996; Halgren, Baudena, Heit, Clarke, Marinkovic, Chauvel, 15
16 et al., 1994; Halgren, Baudena, Heit, Clarke, Marinkovic, & Clarke, 16
17 1994; McCarthy, Nobre, Bentin, & Spencer, 1995; Nobre, Allison, & 17
18 McCarthy, 1994; Nobre & McCarthy, 1994; Smith, Stapleton, & 18
19 Halgren, 1986). N400-like activity has also been observed in intracranial 19
20 recordings from a number of other brain areas, including the middle and 20
21 superior temporal areas picked out by MEG/EROS, and inferior temporal 21
22 and prefrontal cortical areas. The spatial information available from intra- 22
23 cranial recordings is limited by the fact that relatively few recording sites can 23
24 be sampled in any individual (and because the placement of those sites is 24
25 determined by clinical rather than research concerns). However, data across 25
26 such studies suggest that the N400 reflects activity in a distributed set of 26
27 brain regions, including higher order perceptual areas, multimodal proces- 27
28 sing areas, and even emotion and motivation-related areas, such as the 28
29 amygdala. These areas all show activity over a similar time span, between 29
30 about 250 and 500 ms after stimulus onset. 30

31 If the N400 reflects activity in an amodal (or multimodal) semantic system, 31
32 then such activity should be seen in response to the full range of stimuli that are 32
33 associated with meaning. And, in fact, N400s have been recorded to all types of 33
34 linguistic stimuli, including spoken, written, and signed words, and word-like 34
35 items such as pronounceable pseudowords (e.g., pank) and familiar acronyms 35
36 (e.g., VCR) (Holcomb & Neville, 1990; Kutas et al., 1987; Laszlo & 36
37 Federmeier, 2008). N400s are also observed to meaningful but nonlinguistic 37
38 stimuli such as environmental sounds (e.g., animal sounds, telephone ringing; 38
39 Chao, Nielsen-Bohlman, & Knight, 1995; Van Petten & Rieffers, 1995), 39
40 line drawings and scenes (Ganis & Kutas, 2003; Ganis et al., 1996; Nigam, 40
41 Hoffman, & Simons, 1992), faces (Barrett & Rugg, 1989; Bobes, Valdes-Sosa, 41
42 & Olivares, 1994), movies (Sitnikova, Kuperberg, & Holcomb, 2003), and 42
43 gestures (Kelly, Kravitz, & Hopkins, 2004; Wu & Coulson, 2005). Another 43
44 important aspect of the modality-independence of the N400 response is that 44

1 N400 amplitudes are modulated by semantic relationships between stimuli, 1
2 irrespective of stimulus modality or type. That is, the N400 response to a 2
3 picture, for example, can be affected not only by its semantic relationship with 3
4 another picture (Barrett & Rugg, 1990b; McPherson & Holcomb, 1999), but 4
5 also with a visually presented word or sentence (Federmeier & Kutas, 2002; 5
6 Wicha, Moreno, & Kutas, 2003), an auditory word (Pratarelli, 1994) or even a 6
7 smell (Grigor, Van Toller, Behan, & Richardson, 1999; Sarfarazi, Cave, 7
8 Richardson, Behan, & Sedgwick, 1999). Such cross-modal effects are some- 8
9 times weaker than corresponding within-modality ones (Anderson & 9
10 Holcomb, 1995) but persist even when stimuli are masked to reduce the 10
11 contribution of strategic, attentionally driven processing (Eddy, Schmid, & 11
12 Holcomb, 2006; Kiyonaga, Grainger, Midgley, & Holcomb, 2007). Thus, the 12
13 N400 seems to occur at a processing stage that is common across sensory 13
14 modality and stimulus type. 14

15 On the other hand, if the semantic system contains modality-dependent 15
16 as well as modality-independent processing areas, then the source of the 16
17 N400 might be expected to shift for different kinds of inputs or different 17
18 kinds of words. In fact, there are reliable differences in the scalp distribution 18
19 of the N400 elicited by different types of stimuli. N400s to visually pre- 19
20 sented words have a medial, centro-posterior focus and are often larger over 20
21 the right than the left hemisphere (which should not be taken to suggest 21
22 greater involvement from the right hemisphere, as, depending on the 22
23 precise orientation of the electrical dipole, a left hemisphere source can 23
24 elicit electrical activity with a maxima over right hemisphere electrode sites) 24
25 (Kutas & Hillyard, 1982). N400s to auditory words, instead, manifest a 25
26 more central scalp distribution (Holcomb & Anderson, 1993; McCallum, 26
27 Farmer, & Pocock, 1984). Environmental sounds elicit a scalp distribution 27
28 similar to that seen for auditory words, but with a different pattern of 28
29 hemispheric asymmetry. This is consistent with views that posit a left 29
30 hemisphere bias for the processing of verbal stimuli but a right hemisphere 30
31 bias for the processing of nonverbal stimuli (Van Petten & Rieffers, 31
32 1995). N400 responses to pictures and scenes are notably more anterior than 32
33 those to visually presented words (Ganis et al., 1996; Holcomb & 33
34 McPherson, 1994), perhaps reflecting enhanced contributions from brain 34
35 areas involved in visual- or imagery-related processing. Interestingly, a 35
36 similar anterior shift is seen for the N400 responses to concrete, as compared 36
37 with abstract, words (Holcomb, Kounios, Anderson, & West, 1999; 37
38 Kounios & Holcomb, 1994; Lee & Federmeier, 2008). Although the precise 38
39 nature of these distributional differences is not entirely understood, their 39
40 existence suggests that semantic processing samples from partially nonover- 40
41 lapping sets of neural areas for different types of stimuli (and may therefore 41
42 be functionally nonidentical as well; see, e.g., Federmeier & Kutas, 2001), 42
43 consistent with the Hebbian cell-assembly type of accounts of semantics that 43
44 have already been discussed. 44

3.3. The N400 and Conceptual Structure and Flexibility

If the N400 is a marker of processing in semantic memory, then it should reflect the kind of conceptual-level structure uncovered in behavioral studies. The N400 is sensitive to the taxonomic organization of knowledge, as can be seen in ERP studies of sentence verification (with smaller N400s to “animals” than “furniture” in “All dogs are animals/furniture”; Fischler, Bloom, Childers, Roucos, & Perry, 1983). The N400 is also sensitive to category membership in a manner graded by typicality (Figure 2), with greater facilitation (amplitude reduction) for more than less typical category members following a category label cue (e.g., smaller N400s in response to “Collie” than “Bichon Frise” after the cue “DOG”; Harbin, Marsh, & Harvey, 1984; Heinze, Muentz, & Kutas, 1998; Polich, 1985; Stuss, Picton, & Cerri, 1988). More generally, N400 amplitudes are modulated by semantic similarity of many types between stimuli, including shared physical, functional, affective, and cognitive features (e.g., Barrett & Rugg, 1990a,b; Bentin, McCarthy, & Wood, 1985; Holcomb & Neville, 1990; Kellenbach, Wijers, & Mulder, 2000; Zhang, Lawson, Guo, & Jiang, 2006). This sensitivity arises not only when participants are directed to notice or judge similarity, or categorical relations, but also under more implicit conditions. For example, during sentence processing (when participants simply read for comprehension without any overt behavioral task),

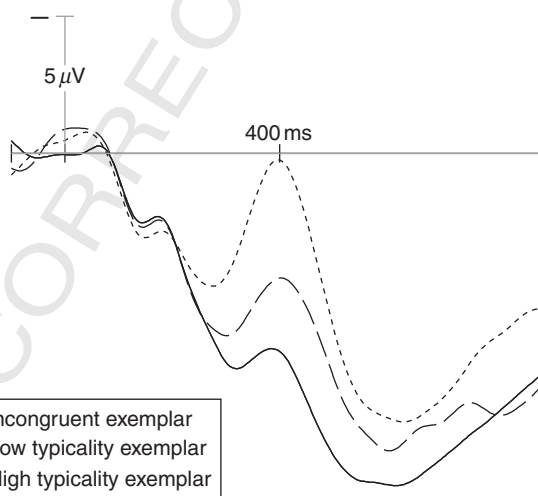
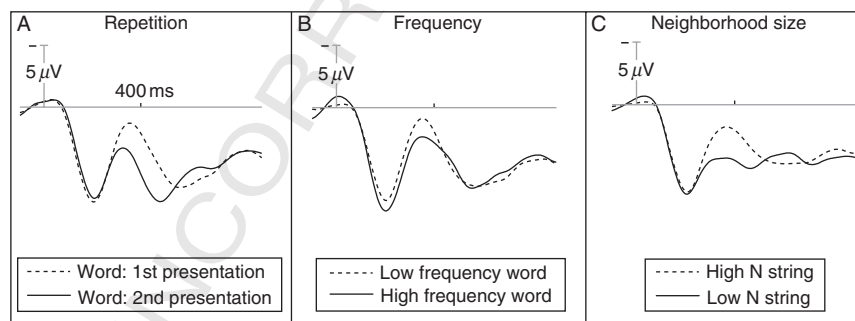


Figure 2 N400 category typicality effects. In response to a category label cue, such as “A type of fruit,” N400 responses are reduced in amplitude to category members (e.g., “apple” or “cherry”) relative to nonmembers (e.g., “penny”) and are more reduced to high typicality (e.g., “apple”) than to low typicality (e.g., “cherry”) category exemplars.

1 categorical similarity to an expected ending produces N400 facilitation for
2 even contextually anomalous sentence completions (e.g., “He caught the
3 pass and scored another touchdown. There was nothing he enjoyed more
4 than a good game of baseball”; Federmeier & Kutas, 1999, 2001). Thus,
5 even when semantic relationships are irrelevant for a particular task situa-
6 tion, N400 processing seems to be influenced by the structure of conceptual
7 knowledge. Finally, N400 effects can be observed even for newly learned
8 categories, with smaller N400s to novel exemplars that share more features
9 in common with the training set (Gratton, Evans, & Federmeier, 2009).

10 Because the N400 is assumed to reflect active processing in semantic
11 memory, it should also be sensitive to dynamic properties of information
12 use—that is, to factors such as the frequency and recency with which
13 conceptual information has been accessed and to the context in which a
14 meaningful item occurs or has occurred in the past. As can be seen in
15 Figure 3, N400 amplitudes are indeed affected by word frequency, with
16 smaller (facilitated) N400 responses to high than to low frequency words
17 (Muentel et al., 2001; Rugg, 1990; Van Petten & Kutas, 1990). As Figure 3
18 shows, the N400 is also sensitive to repetition (Rugg, 1985; Van Petten,
19 Kutas, Kluender, Mitchiner, & McIsaac, 1991) and is modulated by recog-
20 nition memory (Chao et al., 1995; Friedman, 1990; Smith et al., 1986).
21 Furthermore, such effects of memory on the N400 are preserved in amnesic
22 patients (Olichney et al., 2000), who are impaired in episodic—but not
23 semantic—memory. Finally, the N400 is highly sensitive to context;
24 indeed, one of the most important uses of the N400 as a measure has been
25 in studies of context effects in language. N400 amplitudes are modulated by



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39 **Figure 3** Effects of repetition, frequency, and orthographic neighborhood size on the
40 N400. In (A), the N400 elicited by the second presentation of a word in a list format is
41 smaller than that to the first presentation. In (B), higher frequency words elicit smaller
42 N400s than lower frequency words. In (C), meaningless strings with high orthographic
43 neighborhood size elicit larger N400s than those with low orthographic neighborhood
44 size. These factors, along with semantic congruency, comprise the most important
determinants of N400 amplitude.

1 the fit of a meaningful item to its context, whether that context is a single 1
2 word or picture, or a sentence, discourse, or movie (for verbal contexts, see 2
3 review by Kutas & Federmeier, 2000; for nonverbal contexts, see, e.g., 3
4 West & Holcomb, 2002; Sitnikova et al., 2003). Context effects on the 4
5 N400 are graded, with the amplitude of the N400 showing a strong 5
6 negative correlation with measures of contextual fit, such as “cloze proba- 6
7 bility” (the percentage of people who would choose to complete a given 7
8 sentence fragment with a particular word; Taylor, 1953). Thus, the N400 8
9 indexes both the structure and the flexibility that behavioral studies of 9
10 conceptual processing have highlighted. 10

11 12 3.4. The N400: A Neural Marker of Processing 13 in Semantic Memory 13 14

15 In sum, the N400 has all of the properties one would expect of a marker of 15
16 neural activity associated with semantic memory. It reflects activity in a 16
17 distributed, multimodal set of brain areas. This activity seems to be fairly 17
18 automatically elicited in response to a wide variety of types of meaningful 18
19 stimuli. Furthermore, the functional sensitivity of activity in this network 19
20 conforms to both the kind of stability and flexibility expected of concep- 20
21 tual-level processing, showing influences of similarity, typicality, recency, 21
22 frequency, and context. With such a marker, then, it becomes possible to 22
23 address core, outstanding questions about processing in semantic memory, 23
24 such as what types of inputs become linked up to meaning and how, and 24
25 what constraints govern the binding of information into conceptual-level 25
26 representations. 26
27

28 29 30 **4. FROM INPUT TO MEANING** 30 31

32 Our sensory receptors are constantly bombarded with information, 32
33 not all of which is meaningful in nature. This raises the question of which 33
34 stimuli are ultimately selected for semantic processing, and how and when 34
35 that selection takes place. A review of the N400 literature suggests an initial 35
36 answer to this question, as, indeed, not all types of stimuli seem to elicit 36
37 N400 responses. In particular, whereas, for example, visually presented 37
38 words elicit clear N400s, strings of letters that do not follow the typical 38
39 spelling conventions of a language (“illegal strings”; e.g., XQF) do not elicit 39
40 visible N400 activity when presented in unconnected lists (e.g., Laszlo & 40
41 Federmeier, 2007; Rugg & Nagy, 1987). Interestingly, pronounceable 41
42 pseudowords (orthographically regular nonwords, such as GORK) do elicit 42
43 N400s (and show N400 repetition effects) in unconnected lists (e.g., Laszlo 43
44 & Federmeier; Rugg & Nagy), despite also being novel stimuli. This is 44

1 typically explained by the fact that, although pseudowords are not them- 1
2 selves familiar items, they contain many “word-like” features and are thus 2
3 similar to many familiar, meaningful items (e.g., GORK is an orthographic 3
4 neighbor of—that is, shares all but one letter in common with—FORK and 4
5 WORK and GORE, etc.). A similar pattern has been seen for pictures 5
6 (Penney, Mecklinger, & Nessler, 2001), with reduced N400s to repetitions 6
7 of unfamiliar but possible objects (similar to that seen for familiar pictures; 7
8 Eddy et al., 2006) but not to structurally impossible objects. 8

9 This pattern of N400 effects has been interpreted as indicating that access 9
10 to the semantic system may be “gated” in a bottom-up fashion by some 10
11 property of perceptual inputs that makes them likely to be associated with 11
12 information in long-term memory. Hypotheses about what that gating 12
13 property is likely to be and when in processing it might apply differ 13
14 depending on the type of underlying model of recognition that is assumed. 14
15 The following discussion will focus on the recognition of visual words, 15
16 since that has been fairly well studied with electrophysiological measures, 16
17 although similar analyses could be done for semantic access in response to 17
18 auditory words or for objects. 18
19

20 4.1. Models of Visual Word Recognition 20 21

22 The two most prevalent types of reading model in the current literature are 22
23 those that are functionally homogenous and those that instead apply differ- 23
24 ent computations at different levels of processing and to different types of 24
25 items. The so-called “Triangle” model (Harm & Seidenberg, 2004), 25
26 designed to simulate the mapping of orthography to semantics, is a promi- 26
27 nent example from the functionally homogenous modeling tradition. 27
28 It represents orthography, phonology, and semantics in a fully interactive 28
29 manner, using a uniform set of computational principles. In contrast, the 29
30 most recent iteration of the so-called nested modeling tradition, the CDP+ 30
31 model (Perry, Ziegler, & Zorzi, 2007), focuses on linking orthography with 31
32 phonology. Although the CDP+ model is also connectionist, it uses serial 32
33 rather than parallel processing at some of its levels of representation. Also, 33
34 critically, the CDP+ model and other models in its tradition are function- 34
35 ally heterogeneous, in that the computations that are most likely to produce 35
36 the correct pronunciation in response to items with irregular spelling-sound 36
37 correspondence (e.g., YACHT) are separable from those for items with 37
38 regular spelling-sound correspondence (e.g., SHIP). 38

39 In fact, the computational principles embodied in the Triangle and 39
40 CDP+ models mirror the theoretical constructs of a long-standing, primary 40
41 debate in the reading literature. This debate centers on whether or not it is 41
42 necessary to have two functionally (and presumably neurally) separable 42
43 systems in order to account for the ability of fluent readers (at least of 43
44 English) to read aloud both pseudowords and orthographically irregular 44

1 words. Because they are novel, pseudowords presumably cannot be processed 1
2 by “looking up” their phonological representation in a stored database 2
3 of meaningful items (i.e., a “lexicon”), apparently necessitating a system of 3
4 orthography-to-phonology translation rules to explain the ability to pro- 4
5 nounce them. The correct pronunciation of orthographically irregular 5
6 words, on the other hand, could not be obtained through the application of 6
7 those same translation rules, suggesting the need for a direct associative system 7
8 in which orthography is linked to stored information about the word’s 8
9 pronunciation and meaning. This dissociation of systems is supported by 9
10 patterns of deficits observed in dyslexia, with some patients impaired selec- 10
11 tively in the reading of legal nonwords, as in phonological dyslexia (e.g., 11
12 Patient LB; Derouesne & Beauvois, 1985), and others, instead, impaired 12
13 selectively in the reading of illegal words, as in surface dyslexia (e.g., Patient 13
14 MP; Patterson & Behrmann, 1997). 14

15 The model that best typifies theories of word reading that include both a 15
16 directly associative path for illegal words and a rule-based translation for 16
17 pronounceable nonwords is the influential DRC model of word reading 17
18 (Coltheart et al., 2001, also a previous increment of the CDP+ model). 18
19 So-called “dual-route” systems directly map the orthography of words with 19
20 irregular spelling-sound correspondence onto their associated phonology 20
21 (and thence onto semantics). Pseudowords, instead, are translated from 21
22 orthography to phonology by the application of binary, serial, spelling-to- 22
23 sound rules. In such models, orthographic regularity thus serves as a critical 23
24 gating factor, determining which of the two computationally and neurally 24
25 differentiable pathways to meaning a given input can take. 25

26 In contrast, building on the massively interactive, computationally 26
27 homogenous view of word processing originating with, for example, 27
28 Seidenberg and McClelland (1989), a second class of reading models instead 28
29 instantiates a functionally unified system, in which all inputs make contact 29
30 with both phonological and semantic representations. In such models, the 30
31 recognition of irregular words is often accomplished via activity that links 31
32 orthography to semantics, which, in turn, solidifies phonological activation 32
33 patterns. Pseudowords can be recognized using the same computational 33
34 machinery by taking advantage of mappings between orthography and 34
35 phonology developed through prior experience with words containing 35
36 similar parts; for example, the network is able to learn that word-initial K 36
37 is often pronounced /k/ and that word-final AT is often pronounced /æt/, 37
38 and is therefore able to produce the normatively correct pronunciation 38
39 /kæt/, when given the input KAT, without ever having seen that token 39
40 before. 40

41 Though the computations performed to successfully process ortho- 41
42 graphically irregular words and pronounceable nonwords are not identical 42
43 even in models of this tradition, they are functionally homogenous in 43
44 that the same class of computations is performed on every input. Unlike 44

1 dual-route models, therefore, homogenous models do not assign any special 1
2 status to orthographic regularity as a gating factor for word recognition. 2
3 Indeed, the idea that there is *any* such gating factor is somewhat incompati- 3
4 ble with these types of reading models, as it implies that some orthographic 4
5 inputs undergo different computations than others. 5
6

6 7 8 **4.2. Constraints on the Mapping of Inputs to Semantics?** 8 9

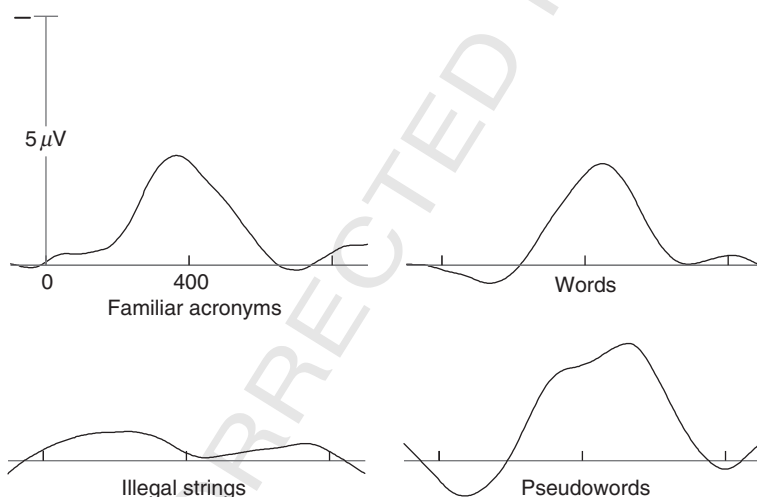
10 Given that the two types of reading models make different predictions about 10
11 when and how different classes of inputs become associated with semantics, 11
12 the N400 would seem a useful measure for deciding between these accounts 12
13 of word recognition. Surprisingly, although some electrophysiological 13
14 work has pointed to orthographic regularity as a filter on N400 processing 14
15 (e.g., Deacon, Dynowska, Ritter, & Grose-Fifer, 2004), few parallels have 15
16 been drawn between questions in the modeling literature about what type 16
17 of computations different input classes undergo and questions in the electro- 17
18 physiological literature about what factors affect the presence and size of the 18
19 N400 response to those same input classes. We therefore set out to specifi- 19
20 cally test models of reading by examining the independent contributions of 20
21 factors like orthographic regularity and stimulus familiarity to semantic 21
22 processing, as indexed by the N400 (Laszlo & Federmeier, 2007, 2008, 22
23 2009). 23

24 We first examined whether or not orthographic regularity gates semantic 24
25 access (as had been previously suggested by Deacon et al., 2004) by compar- 25
26 ing N400 responses to words, pronounceable pseudowords, unfamiliar illegal 26
27 strings, and—a novel stimulus class for this literature—orthographically 27
28 illegal but familiar acronyms (e.g., DVD). As already described, N400 repe- 28
29 tition effects (reduced amplitudes upon second presentation of the input) had 29
30 been seen for words and pseudowords but not illegal strings (Rugg & Nagy, 30
31 1987). This pattern could be explained by assuming that access to semantics 31
32 (as indexed by the N400) occurs only after the perceptual system filters stimuli 32
33 based on orthographic regularity. However, there are also important differ- 33
34 ences in familiarity between these classes of items: words are obviously 34
35 familiar; pseudowords are novel as whole items, but, by virtue of being 35
36 orthographically regular, are also similar to many familiar items; unfamiliar 36
37 illegal strings, in contrast, are neither familiar nor similar to familiar items. 37
38 The inclusion of a familiar class of orthographically illegal items thus opens up 38
39 a means of disentangling the contributions of familiarity and orthographic 39
40 regularity to the observed pattern. Our hypothesis was that if orthographi- 40
41 cally regular and irregular items are processed separately, as suggested by dual- 41
42 route models of reading, we would be able to observe differences in the N400 42
43 elicited in response to orthographically regular and irregular items matched 43
44 for familiarity. In contrast, if orthographic regularity is not a critical gating 44

1 factor, we expected to observe similar N400 responses to both orthographi- 1
2 cally illegal acronyms and familiar, regular words. 2

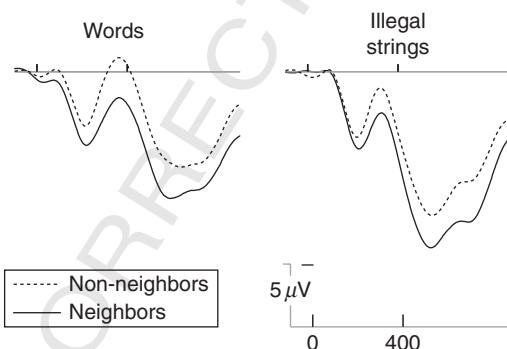
3 In fact, we found that familiar but orthographically illegal acronyms 3
4 elicited N400 repetition effects that were identical in size, timing, and 4
5 distribution to those observed for words and pseudowords (Laszlo & 5
6 Federmeier, 2007; see Figure 4). The results thus suggested that all stimuli 6
7 that are familiar or that contain familiar subcomponents elicit indistinguish- 7
8 able attempts at semantic access. This pattern supports functionally homog- 8
9 enous models over dual-route models that instead propose distinct 9
10 processing pathways gated by orthographic regularity. 10

11 Our more recent work has suggested that not even familiarity is a 11
12 necessary and sufficient prerequisite for the elicitation of an N400, implicat- 12
13 ing a view in which access to semantics is not gated by any specific 13
14 perceptual (or linguistic) property of inputs. Even unfamiliar, orthographi- 14
15 cally illegal items will elicit clear N400 activity when they are presented as 15



33 **Figure 4** N400 repetition effects across stimulus types. N400s are reduced in amplitude 33
34 when stimuli are repeated. Shown here are N400 repetition effects plotted as 34
35 difference waves, which are computed using a point-by-point subtraction of the wave- 35
36 form elicited by the second presentation of an item from the waveform elicited by the 36
37 first presentation of that same item. Difference waves can therefore be conceptualized 37
38 as a continuous time depiction of the effect of repetition. In this figure, repetition effects 38
39 are shown for words (e.g., “DARK”), orthographically regular but unfamiliar pseudo- 39
40 words (e.g., “DAWK”), orthographically illegal but familiar acronyms (e.g., “DVD”), 40
41 and orthographically illegal, unfamiliar strings (e.g., “NKL”). Whereas unfamiliar 41
42 illegal strings fail to elicit N400 repetition effects, familiar illegal strings—acronyms— 42
43 elicit N400 repetition effects that are identical in size, timing, and distribution across 43
44 the scalp to those elicited by words and pseudowords. Thus, orthographic regularity is not a 44
45 requirement for semantic access; instead the degree to which a stimulus is familiar or 45
46 similar to familiar items seems to be the more important. 46

1 completions of highly constrained sentences (e.g., “THEY SAW THE 1
2 LIGHTNING AND HEARD THE NKL”; Laszlo & Federmeier, 2008). 2
3 Furthermore, the N400s to these unfamiliar, illegal items are modulated in 3
4 amplitude by the same kind of factors that modulate N400s to familiar and 4
5 regular items, such as orthographic similarity to an expected completion 5
6 (Laszlo & Federmeier, 2009; see Figure 5). Thus, we have suggested that 6
7 semantic processing is attempted for (and some level of N400 activity thus 7
8 elicited by) all incoming orthographic stimuli, although the degree to which 8
9 this semantic processing will be successful—that is, result in a coherent, 9
10 replicable pattern of activity—will vary with factors such as the type and 10
11 level of contextual support and (indeed) frequency, familiarity, regularity, 11
12 and orthographic neighborhood size, among others. Thus, we do not 12
13 propose that familiarity and regularity have no effect on N400 processing; 13
14 we simply suggest that neither familiarity nor regularity is as critical to the 14
15 elicitation of N400 processing as was once believed. Highly unfamiliar 15
16 stimuli presented out of context may not elicit consistent enough activity 16
17 patterns in semantic memory to, for example, show a benefit from repeti- 17
18 tion. However, when those same stimuli are encountered in rich contexts, 18
19 they can be mapped onto the coherent semantics built from the context, 19
20 allowing their processing to resemble that for familiar stimuli. 20



35 **Figure 5** Orthographic neighborhood effects on the N400. Orthographic neighbors of 35
36 expected, but never presented, sentence completions elicit smaller N400s than do 36
37 orthographically unrelated completions. For example, given the sentence context 37
38 “The genie was ready to grant his third and final . . .,” smaller N400 responses are 38
39 observed to the contextually anomalous word “DISH,” which is an orthographic 39
40 neighbor of the expected completion “WISH,” than to the equally anomalous, but 40
41 orthographically unrelated word “CLAM.” Although illegal strings elicit smaller N400 41
42 responses overall, the same effect holds for the comparison between strings that are 42
43 orthographically related to the expected completion (e.g., “WXSH”) and those that 43
44 are not (e.g., “RQCK”). Thus, it seems clear that, at least in rich semantic contexts 44
such as sentences, even unfamiliar, orthographically illegal strings can elicit N400
activity, which shows a similar functional sensitivity to that for familiar words.

1 Applying a meaning derived from context to an unfamiliar string is a 1
2 highly adaptive action for the language comprehension system to take, as it 2
3 would seem to be a good way to incidentally acquire the meanings of 3
4 unfamiliar words or acronyms—a type of learning that occurs even for 4
5 highly fluent readers throughout the lifespan. Indeed, this is exactly the 5
6 mechanism for word learning assumed by computational theories of seman- 6
7 tic acquisition that utilize latent semantic analysis (LSA; Landauer, Foltz, & 7
8 Laham, 1998). Thus, although the assumption that some inputs are selected 8
9 for semantic processing and others not has a certain degree of intuitive 9
10 plausibility, especially based on models wherein semantic access is a discrete 10
11 stage that follows perceptual analysis, our N400 data suggest instead that 11
12 attempts to access semantic memory might constitute part of the normal, 12
13 default response to sensory inputs of all types. Indeed, in the auditory 13
14 modality, where incoming information is distributed over time, N400 14
15 responses and effects can be observed even before enough information to 15
16 allow identification has accrued (Van Petten, Coulson, Rubin, Plante, & 16
17 Parks, 1999). The view that attempts at semantic processing are obligatorily 17
18 engaged for all inputs, regardless of any particular low-level linguistic 18
19 property, is compatible with massively interactive models of language 19
20 comprehension (Harm & Seidenberg, 2004) and also, more generally, 20
21 with approaches that posit overlap in the computations (and brain areas) 21
22 that underlie what have traditionally been divided into “perceptual” and 22
23 “semantic” aspects of the processing of language (e.g., Barsalou et al., 2003; 23
24 Pulvermuller, 1999; Shallice, 1988). 24

25 26 4.3. Meaning in Context 26 27

28 Semantic information can be derived from individual perceptual stimuli, 28
29 such as words in an unconnected stream of text presented to unwitting 29
30 experimental participants. However, it is perhaps more typical for mean- 30
31 ingful stimuli to occur as part of more complex meaning structures—that is, 31
32 for objects to appear in scenes, words in sentences, or sentences as parts of 32
33 discourses. These higher level structures serve as contexts that can affect the 33
34 perceived meaning of individual incoming stimuli, even as the individual 34
35 stimuli, in turn, contribute to the overall, emergent meaning of the larger 35
36 scale discourse. This interplay between individual inputs and context raises 36
37 the question of how semantic information is integrated across stimuli and 37
38 over time, and whether there are constraints on the levels or types of 38
39 context that can shape the initial semantic processing of an input, as indexed 39
40 by the N400. 40

41 It is well known that stimuli are easier to process if they occur in contexts 41
42 that foreshadow aspects of their semantics, whether those contexts are other, 42
43 individual stimuli (as in semantic priming) or larger meaning structures (as in 43
44 sentence-level congruity effects). However, different mechanisms have 44

1 sometimes been posited for facilitation arising from the semantic similarity 1
2 of an input to an individual contextual element (e.g., a single word) and 2
3 that arising from an input's fit into a higher level representation, such as 3
4 the message-level meaning derived from a sentence or discourse (e.g., 4
5 Forster, 1981; Seidenberg, Waters, Sanders, & Langer, 1984; see discussion 5
6 in Van Petten, 1993b). The former type of facilitation is argued on some 6
7 theories to arise from mechanisms, such as spreading activation, that occur 7
8 rapidly and automatically (without attention). However, the semantic 8
9 representations of higher order language structures cannot possibly all be 9
10 held in memory, as there are an infinite number of possible sentences and 10
11 discourses. Thus, facilitation from sentence and discourse contexts is 11
12 assumed to occur through the application of attentionally controlled pro- 12
13 cesses that integrate information across words and store those integrated 13
14 representations in working memory. 14

15 Mirroring the pattern seen in behavioral measures, N400 responses are 15
16 facilitated—that is, amplitudes reduced—as a function of the semantic fit 16
17 between an item and information provided by an individual prior stimulus 17
18 (Barrett & Rugg, 1990b; Bentin et al., 1985), a sentence or scene (Ganis & 18
19 Kutas, 2003; Kutas & Hillyard, 1984), or a discourse or movie (Sitnikova 19
20 et al., 2003; van Berkum, Hagoort, & Brown, 1999). As already described, 20
21 semantic priming effects on the N400 can be seen even under conditions 21
22 that reduce or eliminate attentional demands and the possibility of strategic 22
23 processing (e.g., Brualla et al., 1998; Deacon et al., 2000; Vogel et al., 1998), 23
24 thus suggesting that they could arise from automatic processes such as 24
25 spreading activation. However, effects in sentences or discourses can be 25
26 seen before the text has been concluded and, indeed, seem to build up 26
27 incrementally (Van Petten & Kutas, 1990, 1991), in line with the hypothesis 27
28 that these effects are tracking the availability of message-level information as 28
29 context accrues. Importantly, when compared directly, word-level and 29
30 higher level context effects on the N400 have been found to be similar in 30
31 their functional sensitivity (e.g., modulation by contextual strength), as well 31
32 as in their timing and scalp distribution (Kutas, 1993; Van Petten, 1993a). 32
33 In at least some circumstances, simultaneous, joint influences of word-level 33
34 and message-level context have been observed (Van Petten; Van Petten, 34
35 Weckerly, McIsaac, & Kutas, 1997). Findings like these suggest that, if word 35
36 and message level context effects do arise from different underlying 36
37 mechanisms, those mechanisms nevertheless have a similar eventual impact 37
38 on relatively early aspects of semantic access. 38

39 However, in addition to these similarities, there are also differences in 39
40 how levels of context impact semantic processing, which are revealing 40
41 of the relative strength and the nature of different information sources. 41
42 As already discussed, N400 amplitudes are sensitive to factors that influence 42
43 the relative ease with which meaning-related information can be gleaned 43
44 from stimuli and, perhaps, also the amount of available information. Out of 44

1 context, N400 amplitudes are smaller to frequent than to infrequent words 1
2 and are reduced by factors, such as repetition, lexical associative priming 2
3 (e.g., bee–honey), and semantic feature overlap (Koivisto & Revonsuo, 3
4 2001; Rugg, 1985, 1990; Van Petten & Kutas, 1990; Van Petten et al., 4
5 1991), which would be expected to ease meaning access. Smaller N400 5
6 amplitudes are also observed for words with low orthographic neighbor- 6
7 hood densities (Holcomb, Grainger, & O’Rourke, 2002; Laszlo & 7
8 Federmeier, 2007, 2008; see Figure 3). One explanation for this pattern is 8
9 that information associated with all items that share a high level of overlap 9
10 with an incoming stimulus tend to become active in parallel. Thus, when 10
11 processing an input (e.g., “BANK”) with many orthographic neighbors 11
12 (e.g., “DANK,” “SANK,” “TANK,” “BARK,” “BUNK,” “BAND,” 12
13 “BANG,” etc.), features associated with all of the neighbors become active 13
14 to some degree, leading to a high level of activity in the semantic system. 14
15 However, when processing an input with a low neighborhood density (such 15
16 as OWL, whose only neighbors are AWL, OIL, and OWN), a much lower 16
17 overall activity level is elicited in the semantic system, leading to smaller 17
18 N400s. A similar explanation has sometimes been put forward to explain 18
19 smaller N400 amplitudes to words with abstract as opposed to concrete 19
20 meaning features (Holcomb et al., 1999; Kounios & Holcomb, 1994). The 20
21 presence of congruent, higher level context information, however, eradicates 21
22 many—although not all—of these effects. 22

23 Word frequency effects, for instance, disappear fairly early on in the 23
24 processing of sentences (Van Petten & Kutas, 1990). It is likely that N400 24
25 amplitudes to words out of context reflect baseline levels of activation, 25
26 which are slightly higher for more frequent words. These baseline levels, 26
27 however, are rapidly overridden by the activity induced as a meaningful 27
28 sentence or discourse is processed. Similarly, although effects of lexical 28
29 association and sentence-level congruity can be jointly observed on words 29
30 in sentence-intermediate positions (when message-level constraints are still 30
31 likely to be low to moderate; Van Petten, 1993a), by the ends of constrain- 31
32 ing sentences even lexical association effects from nearby words are negligi- 32
33 ble (Coulson, Federmeier, Van Petten, & Kutas, 2005; Van Petten, 33
34 Coulson, Weckerly, et al., 1999). Concreteness effects on the N400 are 34
35 also reduced or eliminated for words in sentence contexts (Holcomb et al., 35
36 1999). This set of data thus suggests that message-level semantic constraints 36
37 often have a stronger and longer-lasting impact on semantic activation levels 37
38 than do word-level ones. 38

39 However, higher level contexts do not merely provide a stronger source 39
40 for facilitation than do word-level factors; they actually shape how word- 40
41 level information is processed. Repetition, for example, generally facilitates 41
42 the processing even of words embedded in sentences and discourses 42
43 (Anderson & Holcomb, 2005; Besson, Kutas, & Van Petten, 1992; 43
44 Van Petten et al., 1991), indicating that it is usually easier to re-access the 44

1 semantic features associated with a given perceptual stimulus. However, 1
2 such effects are quite sensitive to context (Besson & Kutas, 1993) and can be 2
3 eliminated or even reversed (Camblin, Ledoux, Boudewyn, Gordon, & 3
4 Swaab, 2007; Ledoux, Gordon, Camblin, & Swaab, 2007; Swaab, Camblin, 4
5 & Gordon, 2004). This occurs, for example, when such repetitions are 5
6 infelicitous, as in the following example: “At the office Daniel moved the 6
7 cabinet because Daniel needed more room for the desk.” This “repeated 7
8 name penalty” seems to arise because information about previously men- 8
9 tioned discourse participants is somehow actively maintained in memory. 9
10 Re-referencing, then, most felicitously occurs through a pronoun, which 10
11 cues the system to use that already active information. Under those circum- 11
12 stances, repetition of a perceptual form creates processing difficulties, rather 12
13 than facilitation, since the system initially assumes that a new participant is 13
14 being introduced. More generally, this pattern emphasizes that the impact of 14
15 lower-level “bottom-up” factors such as repetition seems to depend heavily 15
16 on the current state of the semantic system, as created and maintained by 16
17 context and other higher level factors. 17

18 Finally, there are stimulus-level effects that do not seem to be affected by 18
19 higher level context information. Letter strings with low orthographic 19
20 neighborhood density, such as “VCR,” elicit much smaller N400 responses 20
21 than do strings with more neighbors, such as “FORK” (Holcomb et al., 21
22 2002; Laszlo & Federmeier, 2007, 2008). This is true irrespective of the 22
23 familiarity of those strings; indeed, with other factors held constant the 23
24 N400 response to unfamiliar strings such as “NKH” (low density; very 24
25 small N400 response) or “FUNT” (high density; more negative N400 25
26 response) is identical to that for highly familiar strings with the same 26
27 orthographic neighborhood density, such as “VCR” or “FORK” (Laszlo 27
28 & Federmeier, 2007, 2008). Moreover, this effect of orthographic neigh- 28
29 borhood size seems to be unaffected by the availability of message-level 29
30 information. The pattern seen in word lists, in which items with large 30
31 orthographic neighborhoods elicit larger N400s than items with small 31
32 orthographic neighborhoods (Laszlo & Federmeier, 2007), is also observed 32
33 at the end of even highly constraining sentence contexts (Laszlo & 33
34 Federmeier, 2008, 2009). The notable difference in the effect of context 34
35 on the impact of word frequency versus orthographic neighborhood size 35
36 suggests that the former effect may arise due to activation states in semantic 36
37 memory, which are more transient and malleable, whereas the latter effect 37
38 may arise instead because of how information is organized. If access to the 38
39 semantic system for visual word inputs occurs via representations that are 39
40 organized by orthographic similarity, then neighborhood effects would be 40
41 expected to be fairly ubiquitous. N400 patterns across contexts and tasks 41
42 may thus help provide a means of determining which factors reflect aspects 42
43 of information structure (e.g., orthographic similarity, semantic feature 43
44 overlap) and which reflect the dynamics of information use. 44

5. SEMANTICS “ON TIME”

Overall, then, the pattern across studies points to a semantic system that is shared across modality and stimulus type and that is modulated by information derived both from individual prior stimuli and from higher level structures that are built and maintained over time, as during the processing of a conversation, text, or movie. This system may not be best characterized as fully “amodal” in nature, given observed modality and stimulus-type effects on the scalp distribution of the N400 (and, by inference, the precise configuration of neural generators involved in semantic processing in these cases). However, the binding of meaning to input and between single inputs and context does not seem to be gated by specific perceptual properties or constrained to occur within a particular level or type of stimulus. The ubiquitous nature of semantic processing suggested by electrophysiological data, however, serves to reemphasize the question of how the semantic system can ensure that this diverse, distributed information is appropriately linked up and available when needed.

Although there do not seem to be strong stimulus type or context type constraints on access to the semantic system, electrophysiological data suggest that *time* may be a critical, gating factor for meaning processing. An oft-noted—but little discussed—fact about the N400 is its striking temporal stability. The N400 (to visually presented words) peaks around 375 ms poststimulus-onset in young adults (~20 years old; e.g., Kutas & Iragui, 1998). It is observed later in children (Holcomb, Coffey, & Neville, 1992), and its latency decreases with age and language experience to reach a minimum in early adulthood. Even in adulthood, language proficiency continues to impact N400 latency: in bilingual individuals, N400 responses peak later for the nondominant as compared with the dominant language (Ardal, Donald, Meuter, Muldrew, Luce, 1990; Moreno & Kutas, 2005). N400 latency then increases again after young adulthood at a rate of about 1.8–1.9 ms per year (Kutas & Iragui, 1998). Increased N400 latencies (relative to age-matched controls) have also been noted in conjunction with neurological or psychiatric disorders (e.g., schizophrenia: Grillon, Ameli, & Glazer, 1991; Koyama et al., 1991; Alzheimer’s disease: Iragui, Kutas, & Salmon, 1996; Olichney et al., 2002). Thus, N400 latency clearly reflects something about the neurophysiological state of an individual, which is modulated by anatomical and physiological changes associated with experience, age, and disease.

However, within a given person of a particular age, experience level, and neurological condition, N400 latencies are remarkably resilient to manipulation by psychological factors of the type manipulated in studies of semantic processing. As already discussed, the N400 is sensitive to many stimulus-related variables that have notable effects on reaction times: repetition, word frequency, orthographic neighborhood density, semantic

1 priming, and contextual plausibility, just to name a few. Strikingly, how- 1
2 ever, these variables affect the amplitude of the N400 *but not its latency*. 2
3 Task-related variables that affect, for example, the availability of attentional 3
4 resources, the depth with which stimuli are processed, or the difficulty of 4
5 stimulus selection or stimulus-to-response mapping also affect only the 5
6 amplitude of the N400 (when they have effects at all). 6

7 The temporal stability of the N400 contrasts not only with behavioral 7
8 patterns, where similar types of manipulations to those conducted in ERP 8
9 studies do result in response time differences, but also with effects seen on 9
10 other electrophysiological components linked to stimulus processing and 10
11 evaluation. P300 responses (recall that the P300 was the ERP that compo- 11
12 nent Kutas and Hillyard (1980b) initially expected to see in response to 12
13 semantic anomalies) do shift in latency in response to stimulus and task 13
14 related variables that make stimulus evaluation more difficult (e.g., Kutas & 14
15 Donchin, 1976; Kutas, McCarthy, & Donchin, 1977; McCarthy & 15
16 Donchin, 1981). For example, Kutas, McCarthy, and Donchin (1977) 16
17 asked participants to ~~make three types of classifications of verbal stimuli,~~ 17
18 ~~which varied in their difficulty level:~~ detecting infrequent presentations of 18
19 the name “Nancy” among frequent presentations of the name “David,” 19
20 detecting infrequent presentations of any female name among frequent 20
21 presentations of male names, and detecting synonyms of a particular word 21
22 among frequent presentations of a wide variety of words that were not 22
23 synonyms. When accuracy was emphasized, P300 latencies increased sys- 23
24 tematically with the difficulty of the classification (latest for synonyms and 24
25 earliest for Nancy-among-David), as did response times. Interestingly, 25
26 when speed was instead emphasized, P300 latencies again tracked with 26
27 task difficulty, but reaction times were no longer strongly correlated with 27
28 those latencies. This pattern, along with that seen in other studies, strongly 28
29 suggests that P300 latency reflects stimulus evaluation difficulty, indepen- 29
30 dent of factors that influence the speed with which a response is selected or 30
31 executed (although see Verleger, 1997 for a different view). Indeed, under 31
32 speeded conditions, responses sometimes precede the peak of the P300, 32
33 suggesting that participants occasionally respond before stimuli are fully 33
34 evaluated. 34

35 The behavioral and P300 data strongly suggest that the time needed to 35
36 process and evaluate stimuli varies depending on the nature of those stimuli 36
37 and the context and task environment in which they occur, an idea that 37
38 seems both intuitive and noncontentious. It is thus especially striking that 38
39 N400 latencies do not shift to accommodate task difficulty or context. 39
40 A reasonable (and tantalizing) hypothesis, then, is that the latency of the 40
41 N400 does not vary because its temporal stability serves a functionally 41
42 critical purpose. We posit that this purpose may be to bind—through 42
43 temporal coherence—diverse, spatially distributed information into a 43
44 coincidentally active neurophysiological unit that is experienced as the 44

1 meaning of the eliciting stimulus. This type of temporal binding process is a 1
2 core component of Pulvermüller's (1999) Hebbian cell-assembly view of 2
3 semantics, and similar proposals have been put forward in the context of 3
4 object perception (Hummel & Biederman, 1992; Singer & Gray, 1995; 4
5 Treisman, 1996; von der Malsburg, 1995), attention and consciousness 5
6 (Engel & Singer, 2001; Niebur, Koch, & Rosin, 1993), recall (Damasio, 6
7 1989), response selection (Roelfsema, Engel, Koenig, & Singer, 1996), and 7
8 higher level reasoning (Hummel & Holyoak, 2005; Shastri & Ajjanagadde, 8
9 1993). The N400 may be the scalp manifestation of this temporally synchro- 9
10 nous activity, which should be relatively obligatorily elicited by sensory 10
11 stimuli in all modalities and bear a similar, predictable temporal relationship 11
12 to those stimuli—as the N400 does. Indeed, the medial temporal lobe, 12
13 which, as discussed, seems to be a critical source of N400 activity, is well 13
14 positioned to mediate such temporal binding. It seems to be a shared pinnacle 14
15 of the input stream for visual, auditory, somatosensory, and olfactory infor- 15
16 mation and contains connections to other multimodal processing areas such 16
17 as the frontal lobes and hippocampus (e.g., Brown & Bashir, 2002). 17
18

19 5.1. How When Determines What 19

20
21 The fact that the electrical activity underlying the N400 occurs with a fixed 21
22 temporal relationship to an eliciting stimulus has some important, and 22
23 perhaps surprising, consequences for our understanding of semantic proces- 23
24 sing. First, it suggests that the nature of the initial meaning representation of 24
25 a given stimulus is critically dependent on what information is able to come 25
26 online before the binding process is initiated. Indeed, the field has long 26
27 noted that there are semantically relevant variables that do not seem to 27
28 influence N400 amplitudes. As mentioned briefly already, N400 amplitudes 28
29 are sensitive to hierarchical category relationships, as can be seen in sentence 29
30 verification paradigms. However, in these paradigms, N400 amplitude 30
31 often does not track the truth value of the sentence, patterning instead 31
32 with the association between the subject and predicate. That is, responses 32
33 are identical to “A robin is/is not a tree” (with large amplitude N400s seen 33
34 to both) and to “A robin is/is not a bird” (with smaller amplitude N400s 34
35 seen to both). This result, originally reported by Fischler et al. (1983) has 35
36 been extended to other qualifiers (e.g., all, no, some; Kounios & Holcomb, 36
37 1992) and to information gleaned from pictures immediately following 37
38 verbal prime sentence (“in front of the tower there is a/no ghost”; 38
39 Ludtke, Friedrich, De Filippis, & Kaup, 2008). This pattern is consistent 39
40 with behavioral data and models arising from that data that suggest that 40
41 negation often has a relatively late effect on comprehension (e.g., Kaup, 41
42 Ludtke, & Zwaan, 2006). If information about negation (and other type of 42
43 qualification) becomes available late in comprehension, it cannot influence 43
44 the representation that is formed at the temporally fixed point of the N400 44

1 binding process. The fact that it is timing, and not some inherent property 1
2 of the negation process, that constrains its influence on the N400 is sup- 2
3 ported by data showing that negation does affect the N400 in the sentence- 3
4 picture verification paradigm when there is a long delay between the 4
5 sentence prime containing the negation and the onset of the picture 5
6 (Ludtke et al.). 6

7 Thematic role assignment is another type of information that has, 7
8 perhaps surprisingly, been found not to impact N400 amplitudes (Hoeks, 8
9 Stowe, & Doedens, 2004; Kuperberg, Kreher, Sitnikova, Caplan, & 9
10 Holcomb, 2007; Kuperberg, Sitnikova, Caplan, & Holcomb, 2003). 10
11 For example, Kuperberg et al. (2003) presented participants with sentences 11
12 that included a pragmatic violation, a thematic role violation, or no viola- 12
13 tion, as in: 13

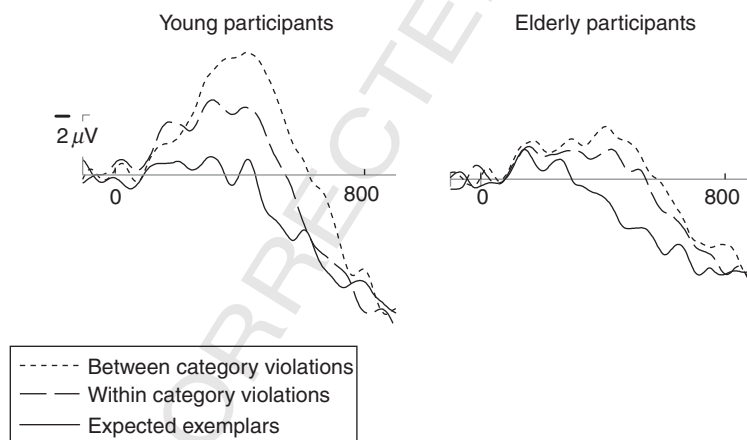
- 14 • Pragmatic violation: For breakfast the boys would only bury . . . 14
 - 15 • Thematic violation: For breakfast the eggs would only eat . . . 15
 - 16 • No violation: For breakfast the boys would only eat . . . 16
- 17

18 N400 amplitudes were larger for the pragmatic violation (“For breakfast 18
19 the boys would only **bury**”) than for the item with no violation, replicating 19
20 many similar findings in the literature. However, N400 amplitudes were of 20
21 similar size for the thematic violation (“For breakfast the eggs would only 21
22 **eat**”) and the no violation item (“For breakfast the boys would only **eat**”), 22
23 despite the fact that the eggs rarely eat breakfast, meaning that the thematic 23
24 violation item is clearly less plausible than the no violation item. The fact 24
25 that pragmatic violations do elicit larger N400s than thematic violations or 25
26 well-formed items suggests that pragmatic information becomes available by 26
27 the time of N400 processing. Most theories would assume that a phrase 27
28 structure has also already been created for the sentence by this point. 28
29 However, it would seem that the time required to map the semantics of 29
30 particular words onto the syntactic phrase structure information in order to 30
31 determine each word’s thematic role exceeds the point at which the N400 is 31
32 triggered. In other words, at the time of the N400, the system does not yet 32
33 seem to be aware that in the thematic violation above, the word eggs is 33
34 being infelicitously bound to the subject role of the eating event (as opposed 34
35 to, e.g., the more plausible object role.) 35

36 Although some kinds of information (such as thematic role) may rarely 36
37 (if ever) be available to influence N400 processing and other kinds of 37
38 information (such as orthographic neighborhood size) may almost always 38
39 be available, there are classes of information whose availability is likely to be 39
40 more variable across people and circumstances. For example, there is a 40
41 growing body of data showing that the brain actively uses context informa- 41
42 tion to predict—that is, to anticipate and prepare to process—features 42
43 of likely upcoming stimuli (DeLong, Urbach, & Kutas, 2005; Federmeier 43
44 & Kutas, 1999; Federmeier, McLennan, De Ochoa, & Kutas, 2002; 44

1 Van Berkum, Brown, Zwitserlood, Kooijman, & Hagoort, 2005; Wicha 1
2 et al., 2003; see review by Federmeier, 2007). As already described, N400 2
3 responses are reduced to “baseball” as compared with “chess” in the 3
4 context of “He caught the pass and scored another touchdown. There 4
5 was nothing he enjoyed more than a good game of . . .” This facilitation 5
6 seems to arise because of the semantic overlap between “baseball” and the 6
7 expected—but never actually presented—word “football.” Indeed, the 7
8 amount of facilitation for words like “baseball” increases proportionally to 8
9 the level of constraint (and thus prediction for) the corresponding expected 9
10 words (Federmeier & Kutas, 1999; Federmeier et al., see also DeLong et al.). 10

11 However, as can be seen in Figure 6, N400 responses to these same 11
12 sentences in older adults do not show the prediction-related pattern 12
13 (Federmeier et al., 2002). This change is consistent with more general 13
14 findings suggesting that older adults become slower and less effective at 14
15 making use of message-level context information during sentence proces- 15
16 sing (e.g., Federmeier & Kutas, 2005; Federmeier, van Petten, Schwartz, & 16
17 Kutas, 2003). If older adults process context information more slowly, then 17
18 prediction-related information may simply not become available in time to 18
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35 **Figure 6** Aging effects on predictive processing, as indexed by the N400. Young 35
36 adults (at left) show N400 facilitation for incongruent sentence-final words that are 36
37 categorically related to an expected (but never presented) completion. For example, 37
38 N400 responses are smaller to “baseball” (a “within category violation”) than to 38
39 “chess” (a “between category violation”) in the sentence context: “He caught the 39
40 pass and scored another touchdown. There was nothing he enjoyed more than a good 40
41 game of . . .” (where “football” is the “expected exemplar”). This pattern points to the 41
42 use of predictive processing mechanisms during comprehension, which preactivate 42
43 features of likely upcoming words—thereby affording a processing benefit to other 43
44 words that share those features. However, as a group, healthy older adults (at right) fail 44
to show this pattern, suggesting that the use of predictive processing during compre-
hension becomes less likely or less effective with age.

1 influence the N400. Consistent with this suggestion, older adults with 1
2 higher verbal fluency—that is, who can generate more words that fit a 2
3 particular category in a set amount of time—actually do show prediction- 3
4 related effects on the N400, similar to younger participants (Federmeier 4
5 et al., 2002). Thus, quantitative shifts in the timing of processing can 5
6 potentially lead to qualitative differences in what particular facets of seman- 6
7 tics come to be linked up with a given input. 7
8

9 5.2. Semantics Beyond the N400 9

10
11 The fact that time, rather than task, seems to constrain the semantic 11
12 information that is initially accessed in response to a given input and, 12
13 moreover, that some critical information may not be available within 13
14 those time constraints strongly suggests that semantic processing should 14
15 not be conceived of as a single, discrete processing stage. Instead, effects 15
16 related to meaning processing would be expected to occur after the N400 16
17 time window as the language comprehension system adds to, subtracts from, 17
18 or otherwise modifies the activation that was established in the initial 18
19 “sweep” of semantic memory during the N400. 19

20 In line with this suggestion, a number of post-N400 semantic effects 20
21 have been documented. One is a posterior positivity that follows the N400 21
22 (seen between about 500 and 800 ms poststimulus onset; see review by 22
23 Kutas, Federmeier, Staab, & Kluender, 2007) that is sometimes referred to 23
24 as a P600 and linked to language (especially syntactic) revision processes and 24
25 sometimes referred to as the Late Positive Complex (LPC) and linked to 25
26 explicit aspects of memory retrieval; whether the “P600” and the “LPC” 26
27 are in fact the same or related effects or whether there are multiple func- 27
28 tionally and neurally different positivities that follow the N400 is beyond 28
29 the scope of this discussion. The critical observation to be made about such 29
30 late language components is that they often show effects of semantic vari- 30
31 ables that fail to influence N400 amplitudes. For example, although the 31
32 thematic role violations (eggs eating breakfast) described in Section 5.1 are 32
33 not associated with larger N400 responses, they do elicit enhanced posterior 33
34 positivities (Hoeks et al., 2004; Kuperberg et al., 2003, 2007). In the 34
35 example discussed earlier, the lexical association between “eggs” and 35
36 “breakfast” that was facilitated on the N400 was later recognized by the 36
37 comprehension system to contain an error with import for meaning, result- 37
38 ing in the elicitation of a late positivity. In other cases, information which 38
39 fails to facilitate N400 responses has its effects on a post-N400 positivity. For 39
40 example, the semantically ambiguous word “organ” will normally prime a 40
41 word associated with one of its meanings (e.g., “kidney,” “piano”), result- 41
42 ing in reduced N400 amplitudes. However, when prior context informa- 42
43 tion biases one meaning of the homograph (e.g., the word “piano” precedes 43
44 the word “organ”), N400 responses to a subsequent target related to the 44

1 other meaning are not facilitated as compared with an unrelated baseline 1
2 condition (Meyer & Federmeier, 2007). Enhanced posterior positivity is, 2
3 however, observed to these subsequent target items suggesting that the 3
4 previously suppressed meaning eventually does become available—just 4
5 not in time to affect N400 processing. 5

6 Other post-N400 ERP responses related to semantic processing include a 6
7 frontal negativity that has been observed in association with active meaning 7
8 selection processes engendered by ambiguity (e.g., Federmeier, Segal, 8
9 Lombrozo, & Kutas, 2000; Lee & Federmeier, 2006). Interestingly, this frontal 9
10 negativity is not observed when context provides disambiguating information 10
11 sufficiently in advance of the ambiguous input (Lee & Federmeier, 2009; 11
12 Van Petten & Kutas, 1987), in which case effects on the N400 are sometimes 12
13 observed instead (Lee & Federmeier, 2009). A frontally distributed positivity 13
14 has also been observed and linked to processes involved in meaning revision 14
15 (Federmeier, Wlotko, De Ochoa-Dewald, & Kutas, 2007). Another aspect of 15
16 the N400's specificity to activity elicited in temporal synchrony with a particu- 16
17 lar input is its general insensitivity to contextual constraint (e.g., Kutas & 17
18 Hillyard, 1984). Some contexts (e.g., “He bought her a pearl necklace for 18
19 her . . .”) lead to fairly strong expectations for particular upcoming words 19
20 (“birthday”), whereas other contexts (e.g., “He looked worried because he 20
21 might have broken his . . .”) lead to much weaker and more varied expectations 21
22 (“arm”?). Thus, the state of the semantic system would seem to be different 22
23 following the presentation of these two context types. However, N400 23
24 responses to unexpected but plausible words (e.g., “collection” in either 24
25 context above) are identical in the two constraint conditions. Thus, although 25
26 N400 amplitudes clearly track whether the context has preactivated meaning 26
27 features associated with a given input, they do not seem to track the activation 27
28 state of other, unassociated meaning features. Unexpected items in strongly 28
29 constraining contexts, however, elicit enhanced frontal positivity that would 29
30 seem to be related to the need to suppress or revise the contextually induced 30
31 expectation for a different word (Federmeier et al., 2007). 31

32 These effects, and others like them, make clear that the meaning of a given 32
33 input and of the higher level context in which it occurs emerges over time as 33
34 the result of multiple kinds of processes (with multiple neural roots). Some of 34
35 these processes, like the N400, seem to be ubiquitous and automatic but 35
36 critically constrained by the timecourse with which different kinds of informa- 36
37 tion become available in different contexts and in different people. Other 37
38 processes, which appear to be recruited in a more strategic and possibly more 38
39 flexible manner as new information becomes available, then serve to update or 39
40 repair the initial meaning representation and to link it in to higher level 40
41 meaning structures. These processes may be subject to less stringent temporal 41
42 constraints than the N400, although at least some models suggest that timing 42
43 and temporal synchrony play a critical role in these higher order meaning 43
44 analyses as well (e.g., Hummel & Holyoak, 2003). 44

6. CONCLUSIONS

The ease with which meaning is experienced belies the critical challenge that constructing that meaning poses to the brain. Although there is not yet a “Dewey Decimal System” of the human brain, studies of patients and work using brain imaging techniques with good spatial resolution have revealed that meaning resides in a complex, spatially distributed neural network. Information must be rapidly accessed from this network, in a manner that is stable and stimulus-driven yet also flexible and context-dependent. And, somehow, these distributed activation states must be reliably linked up with one another, and with the eliciting stimulus, to yield stable, conceptual-level representations. Determining how this comes to be accomplished is arguably one of the central challenges for the development of a neurally and cognitively plausible model of human cognition.

In this chapter we have argued that a central component of any such model will have to be time. Electrophysiological data reveal that activity in a spatially distributed brain network converges around 400 ms after stimulus onset and can be measured at the scalp as a widely distributed negative-going voltage deflection. This N400 activity is elicited by meaningful stimuli of all types in all modalities, in a manner that is sensitive to attention but that does not seem to require attention. Temporal lobe activity seems to be an important source for this scalp-recorded component, although the distribution of the N400 response varies with stimulus type and modality, suggesting that somewhat different configurations of meaning-related information come online in response to different types of inputs. The amplitude of the N400 is sensitive to the full range of variables that would be expected to affect the ease with which an initial semantic representation can be built, including factors such as repetition and frequency and context information of all types and levels. Its latency, however, is remarkably invariant, suggesting that time, and timing, serves as an essential binding force. Time not only seems to bind meaning-related information together, but also to constrain the binding process itself. Information that is not available by the time the temporally constrained binding process is elicited must be incorporated later, as additional processes come online to modify the initial semantic representation. In other words, there is a “time for meaning,” and the fact that semantic information must be *on* time necessitates that the full appreciation of meaning happen *through* time.

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