N400

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The **N400** is a feature ("component") of the human scalp-recorded event-related brain potential (ERP). Its name derives from the fact that the N400 is a negative-going potential (relative to a reference behind the ear), which peaks around 400 ms post-stimulus onset (and is observed between about 250 and 550 ms) in young adults. The N400 forms part of the typical electrical brain activity seen in response to a wide array of meaningful and potentially meaningful stimuli, including visual and auditory words (and word-like strings of letters), acronyms, sign language signs, pictures, environmental sounds, and gestures.

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History

In 1978, Kutas and Hillyard began a series of studies to investigate the influence of sentence contexts on word recognition using event-related brain potentials (ERPs) as a dependent measure. They predicted that encountering an unexpected word would elicit an ERP component today known as the P3b. The P3b is a positivity, largest over posterior regions of the young adult scalp, whose amplitude is inversely correlated with the eliciting item's subjective probability of occurrence: the less probable or expected an item is, the larger its P3b (Donchin, 1981). Kutas and Hillyard therefore designed their initial series of experiments to optimize the likelihood of eliciting a P3b (to better see the effects of contextual manipulations on its amplitude and/or latency). Accordingly, only one-quarter of 160 sentences, each seven items long, ended with a stimulus that was unexpected in some way. For example, along with sensible, congruent control sentences such as "*I shaved off my mustache and beard*" were improbable experimental sentences such as "*I shaved off my mustache and eyebrows*" (congruent but low probability); "*I shaved off my mustache and city* (semantically anomalous)"; "*I shaved off my mustache and [impressionistic artistic picture]*" (novel, uninterpretable); "*I shaved off my mustache and BEARD*" (congruent but physically unexpected); "*I shaved off my mustache and [line drawing of a beard]*" (also congruent but physically unexpected); "*I shaved off my mustache and [line drawing of a city]*" (both semantically anomalous and physically unexpected). In all cases, sentences were presented one word at a time, approximately 1 per second. ERPs were recorded to each word in the sentence, and calculated across the sentence, although the main comparisons were at the sentence final word. On average, all unexpected endings elicited an ERP waveform that was somehow different from the congruent control endings. Physically unexpected endings ("*I shaved off my mustache and BEARD*") elicited the expected P3b. However, semantic anomalies in particular elicited a large, robust negativity (relative to a reference behind the ear on the mastoid process) with a maximum over central-parietal scalp sites, which peaked around 400 ms in young adults; it was therefore called the "N400" (Kutas & Hillyard, 1980a,b,c). This response was thus notably different from a P3b, and subsequent work has established that a given stimulus can elicit both an N400 and a P3b.

Main Paradigms

The fact that in the original publication it was semantic violations that revealed a large N400 response led to an erroneous impression that the N400 might be the neural reflection of a linguistic anomaly or violation detector. This misimpression has been difficult to completely correct, despite the fact that already in the initial publication non-anomalous, albeit less expected, low (cloze) probability items (e.g., "*He shaved off his mustache and eyebrows.*") elicited moderate-sized N400s relative to congruent control sentences (Kutas & Hillyard, 1980c). In fact, the current consensus view is that all potentially meaningful items elicit N400 activity. N400s have been recorded to all types of linguistic stimuli, including spoken, written, and signed words, and word-like items such as pronounceable pseudowords (e.g., pank) and familiar acronyms (e.g., VCR) (Holcomb & Neville, 1990; Kutas, Neville, & Holcomb, 1987; Laszlo & Federmeier, 2008). N400s are also observed to meaningful but non-linguistic stimuli such as environmental sounds (e.g., animal sounds, telephone ringing; Chao, Nielsen-Bohlman, & Knight, 1995; Van Petten & Rheinfelder, 1995), line drawings and scenes (Ganis & Kutas, 2003; Ganis et al., 1996; Nigam, Hoffman, & Simons, 1992), faces (Barrett & Rugg, 1989; Bobes, Valdes-Sosa, & Olivares, 1994), movies (Sitnikova et al., 2008), and gestures (Kelly, Kravitz, & Hopkins, 2004; Wu & Coulson, 2005). Whether or not N400 activity is readily discernable in the scalp-recorded signal will depend on a host of factors including the context and task in which the stimulus is embedded (which, among other things, affects the degree to which overlapping activity might mask the N400 response), as well as various biological factors. However, importantly, this means that nothing special need be done to elicit reliable N400 activity to these types of stimuli. Nonetheless, there are several classes of experimental paradigms that are typically used in the laboratory to elicit N400s and to look at **N400 effects** (i.e., subtractions between conditions revealing N400 amplitude differences). These include priming paradigms and manipulations of sentence or other higher-level expectancies.

Priming paradigms typically include a pair of items (e.g., two words), one of which (usually the one presented first) is the prime and the other of which (usually the one presented second) is the target. The N400 under investigation is that to the target item as a function of its relationship to the prime, as N400 amplitude is sensitive to a variety of types of relationships between the stimuli. In the case of a repetition paradigm, the prime and target are actually the same item; repetition provides a useful means of studying memory incidentally, as well as of comparing the semantic processing associated with different types of stimuli under very similar task conditions. However, non-identical targets and primes are also used, and these can be related in many different ways: categorically, associatively, or otherwise semantically related as in *cat-dog*, phonologically related as in *cough-rough*, visually similar as in *rough-dough*, etc. Pairs may be presented simultaneously (e.g., written one above the other) or one after the other, either at a shorter (e.g., 0-300 ms) or longer (e.g., 500+ ms) interval. In other cases, especially in repetition paradigms, primes and targets may be presented in lists, separated by various numbers of other items (e.g., … *parrot,* ***table****, cat, flower,* ***floor****, mother* …). There can also be more than one prime in some cases – for example, in word triplets, where the critical, target word may be preceded by multiple, related words.

A wide variety of tasks have been used in conjunction with priming paradigms, including reading or listening for comprehension, lexical decision (i.e., determining whether the item is or is not a real word in one's language), relatedness judgments, or, in the case of items presented in a list, monitoring for (and perhaps pressing a button to indicate the presence of) some particular stimulus or stimulus type. In most studies, the prime and target are readily detectable, but in others one or the other may be forward or backward masked such that people are unable to report what they sensed or in some cases even whether a stimulus was presented at all.

N400s are also often examined to stimuli embedded in sentences. These paradigms are on the whole variants of the sentence violation paradigm used in Kutas and Hillyard (1980c). Typically, a sentence is presented one word at a time, each for some duration at a particular rate. Embedded within the sentence – mostly in the final position but in some cases in a sentence medial position – is a stimulus (e.g., word or picture) that renders the sentence nonsensical. Because the nonsensical stimulus cannot benefit from the sentence context information, the response to that item is characterized by a larger N400 (similar to what might be seen out of context) than that to a different, sensible item in the same sentence context, or to the same item in an otherwise "similar" sentence context where it makes sense. For example:

- Sentence final: *I planted string beans in my **garden/sky**.*
- Sentence medial: *Frogs like to eat bugs and other small **insects/radios**, among other ….*

Because semantic violations/anomalies as such are not necessary to elicit an N400, variants of this paradigm manipulate levels of expectancy within plausible sentences, by contrasting stimuli that the context has rendered predictable with either plausible but unpredictable stimuli in those same, relatively constraining contexts (e.g., "*He bought her a pearl necklace for her **birthday/collection**.*") or with stimuli in contexts that provide little basis for expectation (weakly constraining contexts; e.g., "*He looked worried because he might have broken his **collection***").

Written sentences have most often been presented one word at a time, but some have presented groups of words (e.g., "*A robin__is/is not__a bird/car.*"; Fischler et al. 1983); typical (generally experimenter-determined) presentation rates include two words per second and, more recently, three words per second (initial studies used one word per second), although a few studies have employed a variable presentation rate (e.g., different rates for different classes of words). Spoken sentences have been presented both one word at a time and as natural speech. In addition to isolated sentences, sentence pairs and longer discourses have been used in language studies, and cartoon sequences and videos have also served as contexts for non-verbal stimuli.

Factors that influence N400 amplitude

The size of the N400 is typically measured as a peak (minimum value) or, more often, a mean voltage within a time window encompassing 400 ms post-stimulus-onset. Typically, the lower boundary of the time window used to measure the amplitude (or find the peak) is around 250 ms, after the peak of the immediately preceding positivity (P2). Upper time window boundaries beyond about 600 ms (around the time that later positivities, such as the P600 or LPC are typically beginning) would be unusual, particularly in healthy young adults. A 250-550 or 300-500 ms measurement time window is very typical. It is important to note that the N400 is a *relative* negativity – that is, the waveform reaches a local minima around 400 ms. It is not uncommon, however, for the absolute value of the mean or peak N400 amplitude to be a positive voltage (this will depend on stimulus and task properties, as well as the choice of reference and baseline). In what follows, "larger" N400s mean more negative mean/peak voltages and "smaller" N400s mean more positive mean/peak voltages. It is also important to note that the lack of a clear negative-going deflection ("bump") in the waveform cannot be taken as a reliable indicator that N400 activity was not elicited, as N400 effects (i.e., condition-related amplitude differences with functional sensitivity, timecourse, and distribution appropriate for an N400) can be observed even in cases in which the waveform does not contain a clearly delineated N400 peak (see, e.g., Laszlo & Federmeier, 2007).

Although, as will be described later, the timing and the distribution of the N400 are relatively stable, a number of factors have been found to reliably affect the amplitude of the N400, making N400 amplitude a very useful measure for studies of language and memory, among others. As discussed in more detail next, several factors affect the size of the "baseline" N400 (that is, N400 amplitude to stimuli presented in isolation), including, for letter strings, frequency and orthographic neighborhood size. Relative to this baseline state (greatest amount of negative-going activity), then, N400 amplitudes are reduced by factors that might be expected to ease processing, such as repetition, word-level priming, and supportive context information at the sentence or discourse level. These N400 amplitude modulations seem to be fairly implicit in nature and can occur under conditions of reduced awareness; however, the presence and size of N400 effects is affected by attentional allocation.

Frequency

With other factors held constant, words with higher frequency of use in a given language have been found to elicit N400s of smaller amplitude (i.e., to be more positive) than words with lower frequency of use. These effects have been observed for words presented in list format (Rugg, 1990) as well as for words in larger language structures when semantic and syntactic constraints are minimal (e.g., at the beginnings of sentences; Van Petten & Kutas, 1990). Frequency effects, however, seem to fairly readily become overridden by other forms of contextual constraint, such that they are no longer evident, for example, in the middle and end positions of congruent sentences (Van Petten & Kutas, 1990).

Orthographic neighborhood size

The size of a string's orthographic neighborhood – that is, the number of words in the language that share all but one letter in common with that string (Coltheart's N) – affects N400 amplitude, with larger (more negative) N400s elicited by strings with larger orthographic neighborhoods (Holcomb et al., 2002). Different from the effects of frequency, these effects of neighborhood size persist even for strings at the end of constraining, congruent sentences (Laszlo & Federmeier, 2008). For some time, the notably reduced N400 amplitude to low N strings led to a belief in the field that illegal strings – those that do not follow the orthographic conventions of a language and, correspondingly, have very low neighborhood sizes – do not elicit N400 activity at all. More recently, however, it has been shown that familiar but orthographically illegal strings, such as acronyms like DVD or NFL, elicit canonical N400 effects (Laszlo & Federmeier, 2007, 2008) and that even unfamiliar illegal strings elicit clear N400 activity when embedded in sentence contexts (Laszlo & Federmeier, 2008).

Repetition

When items that elicit N400s – including letter strings, pictures, and auditory words and sounds – are repeated in an unstructured list, the second presentation elicits a reduced (more positive) response (Rugg, 1985). Repetition effects are generally largest for immediate repetition and decrease in size with more intervening items/time. N400 repetition effects may overlap with earlier effects of repetition on sensory components, as well as with effects on late positivities that have been linked to explicit recollection. The N400 repetition effect is preserved in patients with medio-temporal lobe amnesia, whose ability to explicitly note the repetitions is severely compromised, pointing to a link between N400 modulations and more implicit aspects of cognitive processing (Olichney et al., 2000).

N400 repetition effects can also be observed for words in higher-level language structures (e.g., Van Petten et al., 1991), and are then influenced by the contexts in which the repeating words occur. For example, repetition effects for words embedded in sentences may be blocked when those repetitions occur in different contexts; this is true even when the meaning of the repeated word is preserved (Besson and Kutas, 1993). When repetitions are infelicitous, as in the context of the repeated name penalty ("*At the office John moved the cabinet because **John** needed more room for the desk.*"), repetition effects may again be blocked and/or unrepeated words may elicit more N400 facilitation than repeated ones (Swaab, Camblin, & Gordon, 2004).

A number of studies have also looked at N400 effects in cross-modal paradigms, in which, for example a word is first seen in the auditory modality and then repeated visually, or vice versa (e.g., Anderson & Holcomb, 1995). Cross-modal repetition does reduce N400 amplitudes, although the presence and size of this effect is affected by factors such as the stimulus onset asynchrony (SOA) between the repetitions and the order of modality of presentation (e.g., visual-auditory repetitions seem to be bigger and more robust across SOA than auditory-visual ones; Holcomb et al., 2005). However, these cross-modal effects have been shown to persist even when stimuli are masked to reduce the contribution of strategic, attentionally-driven processing (Eddy, Schmid, & Holcomb, 2006).

Semantic/associative priming

N400 amplitudes to a target stimulus are reduced (become more positive) when a prior stimulus (prime) has already activated some of that target's features and/or has otherwise rendered the target more expected/predictable, for example because of associations between the prime and target. N400 priming effects have been noted for feature overlap of many kinds, including shared physical, functional, and affective dimensions, among others (Bentin, McCarthy, & Wood, 1985; Kellenbach, Wijers, & Mulder, 2000; Zhang, Lawson, Guo, & Jiang, 2006). These priming effects are graded by factors such as typicality and associative strength (e.g., Harbin, Marsh, & Harvey, 1984; Stuss, Picton, and Cerri, 1998).

N400 priming is seen not only for words in both modalities (Holcomb & Neville, 1990) but for meaningful nonverbal stimuli such as pictures and faces and gestures as well (Barrett & Rugg, 1989; 1990a, 1990b; Wu & Coulson, 2005). And such priming effects seem to readily cross modality and stimulus type. Thus, for example, the N400 response to a target picture can be facilitated not only by its semantic relationship with another picture (McPherson & Holcomb, 1999), but also by a visually-presented word or sentence (Ganis, Kutas, & Sereno, 1996), an auditory word (Pratarelli, 1994) or even a smell (Grigor, Van Toller, Behan, & Richardson, 1999; Sarfarazi, Cave, Richardson, Behan, & Sedgwick, 1999).

As is true of frequency and repetition effects, N400 priming effects are influenced by the context in which they occur. As discussed in more detail below, priming effects and higher-level context effects on the N400 are similar in nature (Kutas, 1993) and can co-occur (Van Petten, 1993). However, when message-level constraints are strong – for example, at the end of congruent sentences – these seem to override word-level priming effects even between nearby words (Coulson et al., 2005).

Expectancy/cloze probability

Since the discovery of the N400, it has been clear that the fit of a word to its sentence context has a critical influence on the N400 amplitude to that word. In fact, cloze probability (e.g., the proportion of people who give a particular word as the most likely completion of a sentence fragment; Taylor, 1953) is one of the most important determiners of N400 amplitude (Kutas & Hillyard, 1984), with high cloze probabilities leading to more strongly reduced (positive) N400s. That such effects reflect the build-up of semantic information over the course of a sentence can also be seen in the finding that N400 amplitudes are systematically reduced with increasing word position over the course of congruent sentences (Van Petten & Kutas, 1990, 1991). The expectancies that drive such effects clearly come from a wide variety of sources including lexico-semantic information and its structure (Federmeier & Kutas, 1999), world knowledge (Hagoort et al., 2004), and information about the speaker (Van Berkum et al., 2008).

These influences of expectancy are not limited to the sentence level. Constraints that arise at the discourse level also reduce N400 amplitudes (St. George, Mannes, & Hoffman, 1994; van Berkum, Hagoort, and Brown, 1999). For example, in the sentence "*Jane told her brother that he was exceptionally **quick/slow** this morning,*" the words *quick* and *slow* elicited N400s of approximately equal size. However, *quick* elicited a smaller N400 than did *slow* when this sentence was preceded by a context sentence that read: "*By five in the morning, Jane's brother had already showered and had even gotten dressed.*" The latency and topography of such discourse-level N400 effects are indistinguishable from those observed within isolated sentences. Expectancy effects can also be seen within nonlinguistic materials, such as for objects and actions in silent movie clips (Sitnikova et al., 2008).

Attention

The extent to which the process(es) indexed by the N400 require attention and/or awareness – that is, are more "automatic" or more "controlled" in nature – has long been of debate. A growing body of data suggests that N400 effects (for example, amplitude modulations resulting from stimulus repetition or semantic priming) can be obtained even when these manipulations are incidental to the task and when the stimuli themselves elicit little conscious awareness. N400 effects have been reported for masked stimuli (Deacon, Hewitt, Yang, & Nagata, 2000; Kiefer, 2002; Misra & Holcomb, 2003), during the attentional blink (Vogel, Luck, & Shapiro, 1998), and during some stages of sleep (Brualla, Romero, Serrano, & Valdizan, 1998). However, manipulations that affect the extent to which attention is allocated to N400-eliciting stimuli do influence the size of N400 effects (e.g., Holcomb, 1988), suggesting that these are not processes that are completely impervious to attention.

Factors that do not influence N400 amplitude

Given the wide range of factors that do influence the amplitude of the N400 to a given stimulus, it is also important to mention factors that do **not** seem to affect N400 amplitude. Manipulations of physical and linguistic variables that do not affect meaning (such as grammatical errors; Kutas & Hillyard, 1983) do not modulate the N400, and N400 effects are also not seen to unexpected events in other structured domains, such as music (e.g., Besson, Faita, Peretz, Bonnel, & Requin, 1998). As discussed next, there are also some manipulations that do have consequences for meaning that nevertheless do not typically or always affect N400 amplitudes.

Contextual constraint

Contextual constraint refers to the power of a context to yield a strong, consistent expectation for a particular upcoming word. Level of constraint is often operationalized as the cloze probability of the most expected word in that context. Thus, a sentence context like "*The paint turned out to be the wrong …*" is strongly constraining for the word *color*, which has a high cloze probability in that context. In contrast, a sentence context like "*He was soothed by the gentle …*" is only weakly constraining; people provide a wide range of completions for this sentence and the most consistent completion, *breeze*, has a low cloze probability.

For the most expected endings of sentences, constraint and cloze probability are the same (as constraint is typically defined). However, both strongly and weakly constraining sentences can be completed by low probability words, allowing a separation of cloze probability and constraint. The word *shade* in a sentence like "*The paint turned out to be the wrong* ***shade***" is thus a low cloze probability completion of a strongly constraining sentence. The word *wind* in "*He was soothed by the gentle* ***wind***" is, instead, a low cloze probability completion of a weakly constraining sentence. With the cloze probabilities of these two ending types matched, one can examine whether N400 amplitudes are affected by the constraint of the sentence context, independent of the cloze probability of the eliciting word. Work crossing several levels of contextual constraint with several levels of cloze probability revealed that N400 amplitude is specifically correlated with the cloze probability of the final word and **not** the contextual constraint of the preceding sentence fragment (Kutas and Hillyard, 1984).

This result makes clear that N400 amplitude does not index the degree to which semantic expectations are violated, which has to be greater for unexpected words in strongly constraining contexts. Instead, N400 amplitudes seem to specifically reflect the degree to which the context information has prepared the processing system for properties of the word eliciting the N400. More generally, the fact that N400 activity seems to be part of the brain's **normal response** to stimuli that cue meaning has important consequences for designing paradigms with the aim of eliciting N400 amplitude changes. Because "baseline" N400 responses are large, factors that ease processing – and hence can reduce N400 amplitudes relative to that baseline – can create readily measurable changes. On the other hand, relative to a case in which a meaningful item is being processed in isolation or in a non-predictive context, creating a "more difficult" processing situation may have little measurable impact on the amplitude of N400.

Negation/quantification

Although the N400 is sensitive to a wide variety of semantic relationships and to constraints based on world knowledge of seemingly all types and sources (Hagoort et al., 2004), N400 amplitudes do not strictly reflect the semantic "truth value" or plausibility of a given expression. When sentences like "*A robin is a* ***tree***" are compared with sentences like "*A robin is a* ***bird***", N400 amplitudes are found to be larger for *tree* than for *bird*. However, when comparing "*A robin is not a* ***tree***" to "*A robin is not a* ***bird***", N400 amplitudes are **again** larger for *tree* than for *bird*, even though in this case it is *tree* that completes a true expression and *bird* a false one (Fischler et al., 1983). Thus, in these simple sentence verification paradigms, N400 amplitudes seem to pattern with the association between the subject and predicate, showing little sensitivity to negation. A similar pattern has also been seen with other qualifiers (e.g., *all, no, some*; Kounios & Holcomb, 1992). However, more recent work from two different laboratories has independently revealed that N400 amplitudes can be modulated by negation, when it is pragmatically licensed (i.e., under circumstances in which negation is normally and informatively used; Nieuwland & Kuperberg, 2008; Staab, Urbach, & Kutas, 2008). Staab et al. (2008) have proposed that pragmatic licensing serves to modulate semantic expectancies, and the accompanying N400; thus, pragmatic licensing can be added to the list of factors that impact N400 amplitude.

Thematic role violations

Other cases in which N400 amplitudes do not pattern with plausibility have been seen in the context of violations of thematic roles -- that is, the linking of a particular word to its grammatical role in a sentence (e.g., subject, direct object, etc.). For example, Kuperberg et al. (2003) compared the response to control sentences (e.g., "*For breakfast, the boys would only **eat** …*") with those to both pragmatic violations (of the type that have been discussed thus far; e.g., "*For breakfast the boys would only **bury** …*") and thematic role violations, such as "*For breakfast the eggs would only **eat** …*". As expected, N400 amplitudes were larger for the pragmatic violations than for the control sentences. However, N400 responses to the thematic role violations were no different from those to control sentences … i.e., N400 amplitudes were equally facilitated for *eat* following *boys* and *eggs* … despite the fact that the eggs rarely eat breakfast, meaning that the thematic violation item is clearly less plausible than the control item. Thematic violations elicited instead a large positivity (P600/Late Positive Complex) that has been more closely linked with syntactic violations. Thus, although the N400 is highly sensitive to expectancy in general, across studies there are a number of cases in which plausible and implausible completions yield similar-sized N400s (sometimes both large and sometimes both small).

Factors that influence N400 latency

Remarkably few factors reliably impact N400 peak onset and/or peak latency to any significant degree. Indeed, many of the factors (e.g., constraining contexts, word frequency, repetition, priming) that influence ease of lexical access/processing – and thus do shorten or lengthen response times to various items – do not typically impact N400 latencies in the same way. Instead, to the extent that such factors do impact the N400 response, it is more often then not by modulating its amplitude. The few factors that have been found to reliably influence the timing of the N400 include age and language proficiency, disease processes, and presentation rate.

Age and proficiency

The N400 to visually presented words generally peaks around 375 ms in healthy young adults (Kutas & Iragui, 1998). It is observed later in children (Holcomb, Coffey, & Neville, 1992), and its latency decreases with age (and presumably language experience) to reach a minimum in early adulthood. Even in adulthood, language proficiency continues to impact N400 latency, as N400 responses have been observed to peak later in a bilingual’s nondominant than in his/her dominant language (Ardal, Donald, Meuter, Muldrew, & et al., 1990). N400 latency then increases again after young adulthood at a rate of just under 2 ms per year (Kutas & Iragui, 1998).

Disease processes

Increased N400 latencies (relative to age-matched controls) have been noted in conjunction with neurological or psychiatric disorders. For example, delayed N400 responses (relative to healthy, age-matched controls) have been associated with Alzheimer’s disease (Iragui, Kutas, & Salmon, 1996; Olichney et al., 2002). There have also been reports of increased N400 latencies in patients with schizophrenia (Grillon, Ameli, & Glazer, 1991; Koyama, Nageishi, Shimokochi, Hokama, & et al., 1991).

Presentation rate

When ERPs are being recorded to visually-presented sentences, words are generally presented at a fixed rate – i.e., with a fixed duration and a fixed SOA between the beginning of one word and the beginning of the next; this is the so-called “rapid visual stimulus presentation (RSVP)” technique, even though it typically isn’t all that rapid. Rapid presentation, however, is one factor that does influence the latency of the N400 effect (measured as the difference between incongruent and congruent words), in a non-linear fashion. With rates between one and four words per second, there is little change in the latency of the N400 effect. However, by 10 words per second, the onset and peak of the N400 effect are delayed by over 75 ms (Kutas, 1993). We don’t yet know what happens to the N400 at different rates of word presentation in speech. In fact, the N400 to words in speech tend to have an early onset and to be less peaked than those during reading, making it more difficult to get accurate latency estimates.

Factors that influence N400 distribution

N400s to visually presented words show a wide-spread scalp distribution with a medial, centro-posterior focus, often slightly larger over electrode sites positioned over the right than the left hemisphere (Kutas & Hillyard, 1982). Note that this should not be taken to suggest greater involvement from the right hemisphere in the elicitation of the scalp-recorded activity because, depending on the precise orientation of the electrical dipole, a left hemisphere source can elicit electrical activity with a maxima over right hemisphere electrode sites. The N400 distribution observed for other stimulus types and modalities is similar, but not identical. For example, N400s to auditory words manifest a more central scalp distribution (Holcomb & Anderson, 1993; McCallum, Farmer, & Pocock, 1984), and environmental sounds elicit a similar distribution but with a small lateral asymmetry that is opposite that for spoken words (left-greater-than-right for sounds, right-greater-than-left for words). N400 responses to pictures and scenes are more anterior than those to visually-presented words (Ganis et al., 1996; Holcomb & McPherson, 1994), and there are also reports of enhanced frontal activity to concrete, as opposed to abstract, words (Kounios & Holcomb, 1994). Such data suggest that semantic processing may sample from partially non-overlapping sets of neural areas for different types of stimuli.

However, assessments of component distributions are complicated by, among other things, the possibility of overlap with temporally contiguous but functionally and/or neurally distinct activity. For example, some have argued that the apparent anterior shift of the N400 to pictures is due to overlap with the “N300”, a frontally-distributed component elicited by line drawings, pictures, and scenes but not (thus far) by words (McPherson & Holcomb, 1999; Holcomb & McPherson, 1994; Hamm, Johnson & Kirk, 2002). Perhaps similarly, emerging work has dissociated the frontal aspect of the response to concrete words from the posterior (more canonically-distributed) N400 activity (West & Holcomb, 2000; Lee & Federmeier, 2008; Huang et al., in press). More work is thus clearly needed to determine the factors responsible for the distribution of the N400 across stimulus and task parameters, and what it implies about the underlying neural source(s) for the activity.

Neural sources of the N400

The wide spread distribution of the N400 would tend to implicate a deep and/or distributed neural source for the scalp-recorded activity. In fact, attempts to model the electrophysiological data in order to ascertain its source have suggested that the scalp-recorded N400 reflects activity in a wide-spread collection of cortical areas (Haan, Streb, Bien, & Rosler, 2000). However, attempting to determine the neural sources responsible for a particular scalp pattern – i.e., solving the so-called inverse problem – is mathematically ill-defined and is particularly difficult to estimate for multifaceted, diffuse sources. Thus, converging evidence from other methods is especially critical. Studies using magnetoencephalography (MEG) and the event-related optical signal (EROS) have fairly consistently pointed to sources in the superior/middle temporal gyrus, the temporo-parietal junction, and the medial temporal lobe, as well as some frontal regions (Helenius et al., 1998; Halgren et al., 2002; Tse et al., 2007). Studies that have recorded activity from both hemispheres have tended to find bilateral activity, although the right hemisphere source may be weaker. Work using intracranial recordings, typically from patients undergoing pre-operative evaluation for epilepsy surgery, have identified a source in the anterior medial temporal lobe that patterns closely with the scalp-recorded N400 in its sensitivity to semantic priming, semantic anomaly, and repetition (Halgren, Baudena, Heit, Clarke, Marinkovic, & Chauvel, 1994; Halgren, Baudena, Heit, Clarke, & Marinkovic, 1994; Nobre, Allison, & McCarthy, 1994; Nobre & McCarthy, 1994). N400-like activity has also been observed in intracranial recordings from a number of other brain areas, including the middle and superior temporal areas picked out by MEG/EROS, and inferior temporal and prefrontal cortical areas. Taken as a whole, the data suggest that the N400 arises from a highly distributed brain network that includes higher-level perceptual areas and multimodal processing and storage areas, perhaps critically in the medial and anterior temporal lobe.

What the N400 has revealed about language processing and cognition

The large body of data about factors that do and do not modulate N400 component parameters notwithstanding, there is to date no consensus on the precise functional significance of the N400. The N400 is often assumed to index some aspect of semantic integration, but a number of different proposals have been put forward over recent years, including hypotheses focused on semantic memory retrieval and binding (e.g., Kutas & Federmeier, 2000; Federmeier & Laszlo, in press), on orthographic/phonological analysis (Deacon et al. 2004), on semantic/conceptual unification (Hagoort & van Berkum, 2007), and on semantic inhibition (Debruille, 2007), as well as the Multiple-cause Intensified Retrieval or MIR hypothesis (van Berkum, in press). Critically, however, even in the face of disagreement about the functional (and neural) particulars, psychological and psycholinguistic experiments using the N400 as a dependent measure have made important contributions to our understanding of language processing and of cognition more generally. Although we cannot do justice to the full range and depth of the empirical and theoretical contributions made from work using the N400, we highlight below a sample of some of the more salient findings and conclusions, which are reviewed in more depth in the papers above and in Kutas et al. (2007).

At the highest level the results from a whole host of studies using the N400 as a dependent measure have offered empirical data regarding (1) what linguistic and non-linguistic factors impact the processing of potential symbols (words, pictures, signs, faces, and gestures, among others) and, critically, (2) when – providing an upper limit on their influence, at least at the level of the neocortex.

More specifically, within the domain of language comprehension, N400 data has provided critical evidence for processing that is immediate, incremental, and graded. The presence of an N400 within 200 ms of the onset of a word that is semantically unexpected in a sentence context is one of the strongest pieces of evidence against any theoretical perspective according to which sentence interpretation is delayed or buffered; i.e., the N400 is a direct brain sign of the immediacy of language comprehension processes during reading, listening, and even signing. And the presence of an N400 to every word in a sentence, with amplitude graded by the build-up of congruent contextual information and by a given word's probabilistic fit to that context (violations forming just one end of the continuum of semantic expectancy), emphasizes the comprehension system's ability to incrementally use partial information in a graded fashion over time as information accrues. Recent data using the N400 as a dependent measure have further provided strong evidence supporting the hypothesis that this use of context information involves the active prediction of features (semantic, morphosyntactic, phonological, orthographic) of likely upcoming stimuli, and that such expectancies can affect the timecourse with which some kinds of information – such as negation – become available to influence processing.

The fact that many variables affect the N400 – from lexical frequency through discourse level contextual information – has offered the opportunity to examine when and how various aspects of the language comprehension system interact. Overall, the findings have argued against strictly serial models of language comprehension, in which words are first analyzed in a bottom-up fashion, with sentence- and discourse-level information available only later in the processing stream. Instead, information of various types and levels (frequency, orthographic neighborhood size, repetition, lexical association, and fit to higher-level contexts of all levels and types) seems to be used in concert and at least somewhat interactively, before the system has completed recognition (as pseudowords and even in some cases illegal strings elicit effects similar to familiar, regular, lexically-represented items). Indeed, although in many ways the N400 is clearly a stimulus-driven brain response, the influence of top-down, context information generally seems to outweigh that from more bottom-up sources (such as frequency, concreteness, and lexical association).

In addition to shedding light on how various language variables interact, work using the N400 has also contributed to the more general understanding of when and how linguistic and nonlinguistic information come together and of the similarities and differences between language and other aspects of cognitive processing. The fact that non-linguistic information elicits N400 activity and that nonlinguistic context information influences the N400 to linguistic stimuli in the same manner as does linguistic context information argues against the idea of a cognitively impenetrable language processing module, at least for certain aspects of word processing, and suggests the need for a broad construal of what can serve as "context" to the language processor. Research in this area has highlighted important functional similarities between sentence processing and the processing of visual scenes, while also pointing to important differences between semantic processing in language and music (which some thought might be more similar).

Finally, studies using the N400 in conjunction with the visual half-field presentation technique (in which stimuli are lateralized to one half of the visual field, biasing their early apprehension to a single cerebral hemisphere) have emphasized the important role played by **both** hemispheres in at least some aspects of language processing, and also have highlighted the differences in the contributions made by each. More generally, N400 data, in combination with that derived from other cognitive neuroscience and neuropsychological techniques, has contributed to the growing understanding of the complex, distributed brain network responsible for language and meaning processing, and of the continuity between perceptual and conceptual levels of processing.

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See also

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