Electrophysiology reveals semantic memory use in language comprehension

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The physical energy that we refer to as a word, whether in isolation or embedded in sentences, takes its meaning from the knowledge stored in our brains through a lifetime of experience. Much empirical evidence indicates that, although this knowledge can be used fairly flexibly, it is functionally organized in 'semantic memory' along a number of dimensions, including similarity and association. Here, we review recent findings using an electrophysiological brain component, the N400, that reveal the nature and timing of semantic memory use during language comprehension. These findings show that the organization of semantic memory has an inherent impact on sentence processing. The left hemisphere, in particular, seems to capitalize on the organization of semantic memory to pre-activate the meaning of forthcoming words, even if this strategy fails at times. In addition, these electrophysiological results support a view of memory in which world knowledge is distributed across multiple, plastic-yet-structured, largely modality-specific processing areas, and in which meaning is an emergent, temporally extended process, influenced by experience, context, and the nature of the brain itself.

Human brains are storehouses of vast amounts of different kinds of information – about people in the neighborhood and in the movies, about places and how to look, reach or navigate towards them, and about things and what they look, sound, feel, smell and taste like. Behavioral studies of categorization have revealed much about the structure of this knowledge, showing that people seem to consistently group together items that share perceptual and functional features in common and that often bring one another to mind. The neurons that respond to these features are found in multiple, hierarchically organized, richly interconnected anatomical areas, all devoted to analysing the same physical inputs in parallel, but each specialized for certain features which may by laid out along a map of the body's surface or of the surrounding environment. Information is rapidly retrieved from this knowledge base, known as 'semantic memory', often in response to a linguistic cue in the form of a spoken, written or signed word. Remarkably, in only hundreds of milliseconds the brain of a language user can make sense of a complex, inherently meaningless signal – that is, a word – using information gleaned from the ongoing discourse and from the environment via sensory processing. Uncovering the psychological and neural mechanisms that support such complex, yet seemingly effortless, meaning processing lies at the very heart of an understanding of human cognition.

Many different types of methods, from the analysis of language patterns in text databases to the measurement of reaction times in intact and brain-damaged individuals, have been directed at determining what meaning is and what semantic information is extracted during language comprehension. One would also like to know how the normal brain constructs meaning and how it does so in real time. These brain processes have remained elusive to behavioral methods and are too fast to be captured by hemodynamic-based brain imaging methods (as elaborated in Box 1). Thus, we focus here on recent findings derived from a high temporal resolution technique that is both a sensitive measure of real-time language processing and a direct manifestation of brain activity: event-related potentials (ERPs). Scalp-recorded ERPs measure the brain's electrical activity, primarily summed post-synaptic potentials of synchronously activated pyramidal cells in the neocortex, that is triggered by an event, such as a word (see Box 1). Analysing changes in the size, timing or distribution of this activity over the head across different experimental conditions provides millisecond-level information about sensory, perceptual, cognitive, and motor processing across different brain regions.

ERPs are especially useful for the study of language comprehension because a negative component peaking around 400 ms after stimulus-onset (the N400) has been shown to vary systematically with the processing of semantic information.

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Box 1. ERPs and other neuroimaging techniques

Among the various kinds of brain signals that can be imaged non-invasively, the most direct and immediate are electrochemical. Neural signaling takes places via the flow of charged particles across neural membranes, which generates an electric potential in the conductive media inside and outside the cell. These synaptic currents can be monitored by placing at least two electrodes somewhere on the head and amplifying the voltage difference between them. The resulting EEG observed at the scalp is due to the summed (postsynaptic) potentials of multiple neurons acting in concert. In fact, much of the observed activity at the scalp probably arises from cortical pyramidal cells whose organization and firing satisfies the constraints for an observable signal (see, for example, Ref. a for more detail).

The changes in field potentials that are time-locked to a sensory, motor or cognitive event are known as event-related potentials (ERPs). A single ERP is too small to be seen by eye but can be extracted from the EEG by averaging the responses to multiple occurrences of similar events. The result is one voltage waveform in time at each recording site, consisting of negative and positive-going deflections, relative to the pre-event voltage activity.

Voltage deflections within the first 200 ms of an event's processing have a characteristic pattern that varies with the sensory modality of the eliciting event, whereas those occurring later vary more with the nature of the cognitive processing engendered by the task. ERP 'components' are typically defined by their timing, scalp distribution, and pattern of sensitivity to experimental manipulations, and, in a few cases, by their neural generators. These components provide useful dependent variables, as their presence, amplitude (size), timing, and/or distribution over the scalp can reveal much about the timing and nature of the neural and cognitive processes engaged.

The electrochemical signals that underlie the ERP create cellular energy demands that are met by increased blood flow to active areas and increased levels of oxygenated blood in the area of active tissue. Imaging methods such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) can localize such metabolic/hemodynamic changes with a much higher level of spatial resolution than can be achieved by electromagnetic measures, at least without additional constraints (Ref. b). Although these hemodynamic-based methods are thus useful for determining which brain areas change their activity levels during experimental manipulations, none of them have the temporal resolution (on the order of tens or hundreds of milliseconds) needed to track the use of semantic memory during language comprehension in real time. The hemodynamic response not only lags behind the eliciting electrical activity by 1–2 s but also is temporally extended across several (5–15) seconds even for a brief electrical impulse and sums non-linearly in response to multiple events occurring within milliseconds or seconds. Even with the development of methods for undoing this sort of overlap (such as event-related fMRI), hemodynamic methods are by their nature limited in their temporal resolution to events occurring at no less than a second.

References

a Kutas, M. and Dale, A. (1997) Electrical and magnetic readings of mental functions. In *Cognitive Neuroscience* (Rugg, M.D., ed.), pp. 197–242, Psychology Press

b Dale, A.M. and Sereno, M.I. (1993) Improved localization of cortical activity by combining EEG and MEG with MRI cortical surface reconstruction. *J. Cogn. Neurosci.* 5, 162–176

This electrophysiological response was first observed by Kutas and Hillyard[1] in response to a semantically anomalous word in a sentence context, such as *city* in the sentence '*He shaved off his mustache and city*'. To date, it has not been observed to incongruities in other settings, such as music[2], nor to anomalies in language that are non-semantic in nature such as grammatical violations[3] or language-irrelevant changes in the physical attributes of words[4]. Although it is especially large to semantic violations, the N400 is not simply an index of anomaly, but rather a part of the brain's normal response to words (in all modalities) or word-like stimuli, such as pronounceable pseudowords[5]. Between 250 and 500 ms after the presentation of a potentially meaningful event, therefore, several brain areas seem to be engaged and their summed postsynaptic activity is observed at the scalp as a negative-going wave referred to as the N400. The amplitude of this response varies systematically with the processing of potentially meaningful stimuli at the level of meaning, being reduced by a variety of factors that increase these items' predictability in the local context (Fig. 1). The N400 has been used as a dependent measure in sentence processing studies primarily to look at the timecourse of context effects and in single word or word pair studies to look at aspects of access into long-term memory (repetition, categorization). Here, we review recent findings in both arenas. We then turn to studies which have brought them together with the aim of delineating how and when long-term semantic memory is used during language comprehension and thereby revealing more about the nature of the psychological and physiological processes underlying the N400.

The N400 and context

The amplitude of the N400 to a particular word is highly sensitive to the immediate context in which it occurs, whether that context is a single word, a sentence, or a discourse. For example, N400 amplitude varies with semantic relationships between individual words in lists, when the words are attended[6–8]. Prior occurrence of an associatively related item (e.g. *bee*) or a semantically related item (e.g. *sugar*) reduces the N400 amplitude to a given word (e.g. *honey*) yielding a 'semantic priming' effect. This N400 reduction is similar in time course and scalp distribution to that observed to words in sentences[9,10], where N400 amplitude is an inverse function of the word's rated 'cloze probability'[11] – that is, the proportion of individuals who provide that particular word as the most likely completion for that sentence fragment in a paper and pencil test[12]. When both sentence context information and word association information are available, they exert partially independent influences on N400 amplitude, indicating that sentence context effects are not simply the sum of word level associations[10]. In fact, N400s are reduced by global, discourse-level constraints as well[13]. van Berkum *et al.*[14], for instance, found that words that were equally acceptable (and elicited equivalent N400s) in an isolated sentence (e.g. '*The mouse quickly/slowly returned to its hole.*') elicited an even smaller N400 if they were coherent (*quickly*) as opposed to incoherent (*slowly*) with extant discourse level constraints (e.g. '*The cat entered the room suddenly, startling a mouse which had found a bit of cheese in the corner.*').

N400 effects thus seem to reflect constraints arising from several levels of context; words that are easier to process because they are expected in a context or are related, semantically, to recently presented words elicit smaller amplitude N400s relative to the same words out of context or in weak or incongruent contexts, respectively. Based on these findings, the prevalent view of the N400 is that it reflects 'contextual integration'[8,15,16]. This view emphasizes the importance of the fit between the eliciting item and context-based information currently held in working memory. Integration is easier, and N400s are correspondingly reduced in amplitude, when the features of a word are coherent with – that is, fit – the local context. One commonly used measure of this ease of integration comes from individuals' plausibility judgments – that is, their subjective sense of how much an item 'makes sense' in a given context. This proposal, then, would predict a close correlation between N400 amplitude and plausibility. As we will show, this is only sometimes the case, suggesting the need for a revised view of how the brain constructs meaning during sentence comprehension.

The N400 and memory

In addition to its sensitivity to local context information during language comprehension, N400 amplitude also seems to be sensitive to the ease of accessing information from long-term memory. For example, N400 amplitudes to words presented out of context vary as a function of even non-semantic factors, like frequency of usage, that arguably reflect something about how readily information associated with these perceptual forms can be accessed from lexical memory. N400 amplitudes also are reduced by repetition, in a manner that varies with both their number and timing[17], and by factors affecting recognition memory[18,19]. This link between the N400 and long-term memory access is bolstered by intracranial recordings showing that at least part of the source for the scalp-recorded N400 are brain areas, such as the medial temporal lobe, known to be crucial for long-term memory processes[20–25].

A specific link between the N400 and long-term semantic memory was first made using the sentence verification paradigm, wherein participants are asked to judge the accuracy of simple statements about category membership such as '*A carrot is a vegetable*'. N400 amplitude was found to be sensitive to such category membership relations regardless of the truth value of the statement[26–30]. That is, N400 amplitudes were reduced when the exemplar was a member of the category, in both affirmative and negative statements (e.g. equivalent N400s to vegetable in '*A carrot is a vegetable*' and '*A carrot is not a vegetable*'). This was the first example of a case in which the amplitude of the N400 did not vary strictly with the plausibility of the item in the local context. Thus, something about the relationship between items in long-term memory seems to influence the neural processes by which brains process sentences. These 'sentences', however, were merely statements about category relationships, leaving open the question of whether such long-term memory organization also influences processing when it is incidental – for example, when categorical relationships are neither mentioned nor needed to understand the sentence.

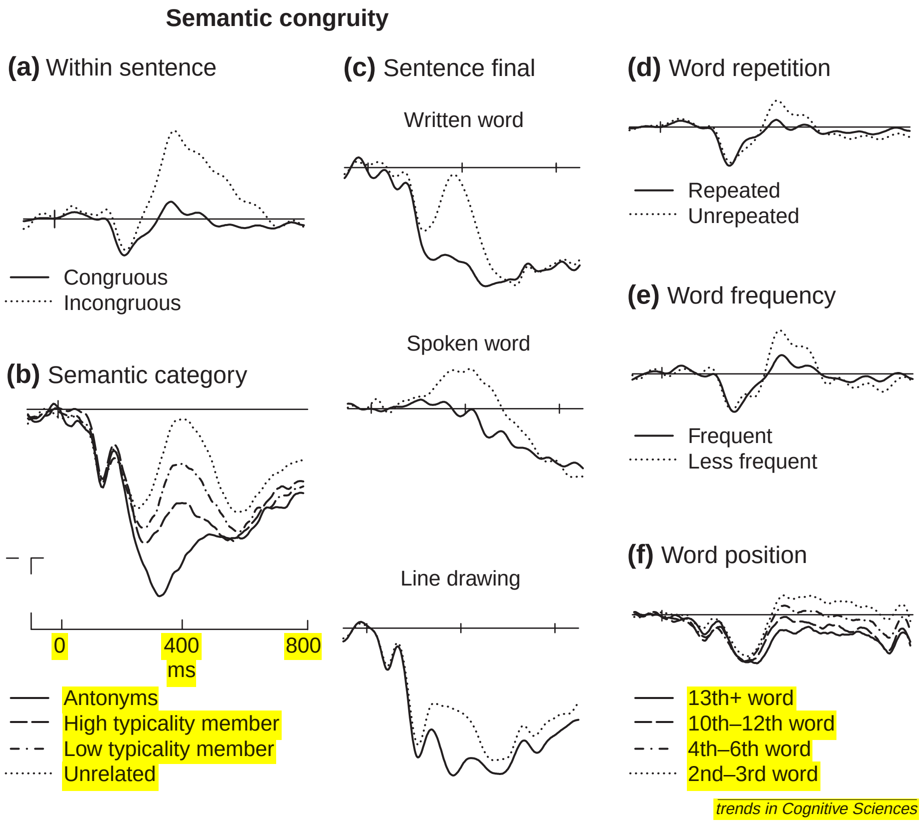

Fig. 1. Factors influencing the N400 response. N400 amplitudes are influenced by a number of different factors, several of which are shown here at a right-hemisphere site approximately over Wernicke's area (homologue). The N400 is highly sensitive to semantic (though not just semantic) relationships of various kinds. **(a)** Incongruous words elicit large N400 amplitudes relative to words that are congruous in their context, whether these items occur mid-sentence or in sentence final position. As shown in **(c)**, this effect can observed in all modalities, including written and spoken words, and line drawings (here, all using the same experimental material). **(b)** The N400 is similarly sensitive to varying degrees and types of semantic relationships in more minimal contexts, including word pairs. Shown are responses to highly constrained antonyms (e.g. *the opposite of black… WHITE*), high typicality category members (e.g. *A type of bird… ROBIN*), lower typicality category members (e.g. *A type of bird… TURKEY*) and to unrelated/mismatched items. **(d)** Mid-sentence words that are repeated in on-going text and show reduced N400 amplitudes, as do mid-sentence words that are more frequent in the language in general **(e)**. The amplitude of the N400 also reflects the build-up of contextual constraint over the course of a sentence **(f)**. Not shown here, the ERP to a word during the N400 epoch (200–500 ms) is also sensitive to relationships at the level of orthography, phonology and morphology (reviewed in Ref. 61).

We addressed this question by setting local, context-based plausibility and long-term memory organization at odds[31]. Specifically, we compared the response to congruent sentence completions ('expected exemplars') with the response to two types of equally incongruent completions: those that came from the same semantic category as the expected completion ('within category violations') and those that did not ('between category violations') (Fig. 2). Although equally plausible, the within category violations share more features in common with the expected exemplar than do the between category violations. For example, palms and pines are both trees that are tall, green year round, drop something to the ground, have slender, needle-like leaves in clusters and edible parts, and provide oil. The expected exemplar also shares some features with the between category exemplar, just not as many. In any case, neither unexpected ending is plausible within the local context and thus the two should elicit the same-sized N400 on the view that the N400 reflects only integration with recently activated information in working memory. However, as can

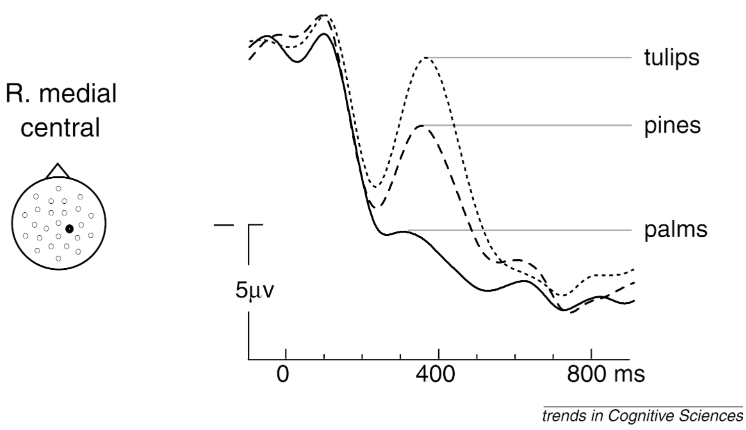

Fig. 2. The influence of plausibility and memory organization on the N400 response to words in sentences. EEG was recorded from 26 scalp electrodes (see head icon) as 18 participants read sentences, like the example shown here, for comprehension. Sentence-final target words included: (1) expected exemplars, the highest cloze probability completions for the sentence contexts (e.g. palms); (2) within-category violations, unexpected (cloze probability <0.05) and implausible (as assessed by plausibility ratings) completions that came from the same basic-level semantic category as the expected exemplars (e.g. pines); and (3) between-category violations, unexpected and implausible completions that came from a different (but related) semantic category (e.g. tulips). Across the experiment all items appeared in all target conditions, although a given participant saw each only once. Data from a representative site over the right, medio-central part of the head is shown (indicated by the filled circle on the iconic head). All unexpected items elicited increased negativity between 250–500 ms post-stimulus onset (N400) relative to the expected exemplars (solid line). However, despite equivalent cloze probabilities and plausibility ratings, the N400 response to the two unexpected items differed as a function of their semantic similarity to the expected completions. Within-category violation (dashed line), which shared many semantic features in common with the expected exemplars, elicited smaller N400s than did between-category violations (dotted line), which had less semantic feature overlap. The results suggest that plausibility alone does not determine the amplitude of the N400 response to words in sentences; semantic memory organization also plays an important role in determining the facility with which the brain processes meaning information on-line.

be seen in Fig. 2, this is not the case: although both elicit larger N400s than expected endings, those to within category violations (e.g. *pines*) are significantly smaller than those to between category violations (e.g. *tulips*). This pattern of data shows that the physical, functional, and perhaps situational similarity between two members of a semantic category affect language processing, even when these relationships do not alter the items' subjective plausibility in the sentence.

Semantic memory in on-line processing

It seems, then, that both the immediate language context held in working memory and the context-independent relationships between items in long-term semantic memory affect the neural processes reflected in the N400. It is of course not surprising that memory is used during sentence processing, for how could it be otherwise? What may be surprising to at least some readers, however, is first that information currently active in working memory (fit to local context) and information accessed from long-term memory exert their influence at about the same time and also apparently act on the same neural processes, those reflected in the N400. Second, these results show that it is not just the contents but also the *organization* of long-term semantic memory that affects language processing on-line. Moreover, this organization does not become relevant just when other cues are less available – for example, when the local sentence context is fairly weak. Instead, we found that the impact of semantic memory organization is actually more pronounced when contextual constraint is strong. That is, the N400 amplitude reduction to within relative to between category violations is bigger in high than in low constraint contexts, as illustrated in Fig. 3. Note that this pattern goes in the opposite direction from the rated plausibility of these items and the opposite direction from patterns in behavioral measures (in similar materials) collected at the sentence end[32,33]. By offering a window into neural activity not directly reflected in behavioral measures, ERPs thus reveal that aspects of the brain's processing of a given word are affected by more than just its fit to the current representation of preceding context held in working memory. Instead, N400 amplitudes to the within category violations seem largely to be a function of the plausibility of the (not actually presented) expected exemplars, suggesting a strong functional link between them.

The functional link between these two categorically related items suggests that the organization of sensory, motor and higher-order features in the brain built up of years of experience with the world (i.e. semantic memory) has an inevitable impact on the neural processes by which brains make sense of language in real time; it determines how brains interpret sensory inputs. So, although *baseball* is neither expected nor very plausible in a sentence wherein the expected exemplar is *football* (as in Fig. 3), it is still a more understandable mistake than a board game (*monopoly*). Like football, baseball is a professional team sport with a ball, played with religious fervor in the USA, characterized by personalities with astronomical salaries. Home runs and touchdowns are alignable features of the two games, both important for scoring, for statistics, for getting the crowd to cheer, etc. The fact that these items share many such features in common in the world makes them easier to process in language when one unexpectedly replaces the other. Moreover, this pattern of effects suggests that the brain uses sentence context information to *predict* (i.e. to anticipate and prepare for) the perceptual and semantic features of items likely to appear, in order to comprehend the intended meaning of a sentence at the fast speed with which it usually comes. The featural overlap between a sentence-final within category violation (e.g. *pines*) and the item expected in the context (e.g. *palms*) could affect processing only if the features of the expected item are already activated in the mind of the comprehender, as this expected item is never actually presented. Thus the very words that determine sentential constraint also determine the strength and precision with which the features of the expected exemplar can be pre-activated in semantic memory before any sentence ending is presented.

Recent work by Van Petten *et al.*, using an auditory sentence comprehension task, further supports this idea[34]. They observed ERP differences between congruent and incongruent sentence completions within 200 ms after word onset, before the auditory signal was sufficient to uniquely identify the words (as determined by a gating study). Furthermore, the N400 to incongruent words that shared initial phonemes with the expected completions (e.g. *captive* when *captain* was expected) deviated from that to the expected item significantly later than did the N400 to incongruent words which did not share initial phonemes. On a purely plausibility-based integration account, semantic processing cannot begin at least until a word is identified and its meaning accessed. Prior to word identification, listeners obviously compare whatever incomplete acoustic information they might have with an expectation (semantic and perhaps even phonological) derived from the context.

It would seem, then, that the language comprehension system makes use of all the information it can as early as it can to constrain the search through semantic memory and facilitate the processing of the item(s) most likely to appear. Such a predictive strategy allows for more efficient processing when the expectation is upheld, presumably accounting for the beneficial effects of a congruent context such as the faster processing, the better memory, and the greater perceptual accuracy when the expected item is somehow degraded or garbled. However, when the expectation is not upheld, the result is a contextual integration problem which may necessitate more processing resources, albeit seemingly less if some of the features of the unexpected item that is actually presented are already active. Prediction is thus an effective comprehension strategy except when it is misleading, as in the case of the within category violations, in which case a 'wait-and-see' integrative strategy would be preferable. This may be one reason that the language comprehension system appears to employ both predictive and integrative strategies, distributed across the two cerebral hemispheres.

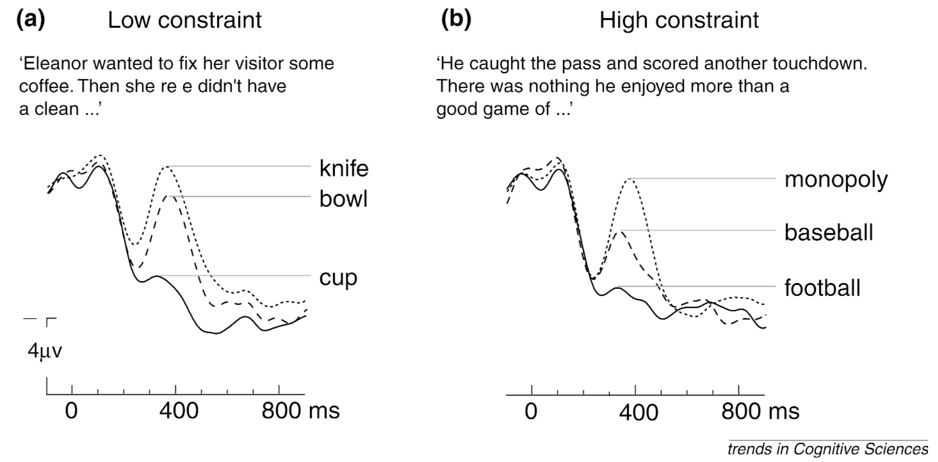

Fig. 3. The interaction of memory organization and contextual constraint. Sentences were sorted into constraint categories based on the cloze probability of the expected exemplar. Low constraint sentences **(a)** had best completions with cloze probabilities under 75%, whereas high constraint sentences **(b)** had best completions with cloze probability 75% or higher. Thus, high constraint sentences tended to lead individuals strongly to expect a single completion, whereas expectations in low constraint sentences were weaker and more variable. Violations of both types (within and between category) were rated as less plausible in high as compared with low constraint sentences. As can be seen here at one representative channel (right medial central), N400 amplitudes to expected exemplars (solid lines) and between-category violations (dotted lines) did not differ as a function of constraint. The response to within-category violations (dashed lines), however, was significantly smaller (more like the response to expected exemplars) in high-constraint contexts than low. This effect goes in the *opposite* direction from the rated plausibility of these items in these sentence contexts. The results therefore suggest that semantic memory organization has an inevitable impact on language processing and that the strength of that impact is positively correlated with contextual strength, and therefore the strength with which the expected item can be predicted and pre-activated.

We used a visual-half-field experimental design with the same stimuli to compare and contrast semantic processing in the left and right hemispheres[35]. As can be seen in Fig. 4, responses to stimuli presented in the right visual field (i.e. initially to the left hemisphere) mirrored those seen with central presentation, indicating a predictive strategy. Responses to stimuli presented in the left visual field (to the right hemisphere) also show a clear effect of contextual fit, namely, large N400s to incongruous relative to congruous completions. However, in this case there is no influence of categorical structure (i.e. no difference between within and between category violations), which is more in line with a purely plausibility-driven strategy. Overall, these results show that the two hemispheres use semantic memory differently during sentence comprehension, with left hemisphere processing seeming biased towards efficiency and prediction and right hemisphere processing biased towards information maintenance and integration with working memory.

Representation in semantic memory

Recent work using the N400 as a dependent measure thus has revealed several important aspects of how semantic memory may be used during comprehension. Naturally, we would also like to know more about the nature of meaning representation in the brain. One primary question is how information associated with different types of stimuli (abstract and concrete words, pictures, faces, sounds) are stored in and accessed from memory. Is there a single, common 'amodal' store accessed equally by all meaningful stimuli (as has been suggested in both the psychological and neuropsychological literatures[36–39]), or does each type of stimulus access its own, modality-specific knowledge base? As ERPs provide information about the strength, timing and neural bases of processing, they also can speak to these issues of representation.

In fact, the processing of almost any type of meaningful, or potentially meaningful, stimulus seems to be associated with negativity between about 250 and 500 ms post-stimulus-onset ('N400'). This is true for not only visual and auditory words, as already discussed[5], but also for line drawings[40–43], photographs[44], faces[45–47], environmental sounds[48,49], and even odors[50,51]. Just as for words, the negativity to these other types of potentially meaningful stimuli is reduced as a function of associative, semantic, and repetition priming and fit to context, whether the context is in the same or a different modality. Auditory words, for example, have been found to prime visual word processing[52], meaningful environmental sounds prime auditory word processing (and vice versa)[48], visually presented sentence contexts prime the processing of line drawings[40,42,43], and even odors prime picture processing[50,51]. The temporal and functional similarity in the electrophysiological responses across stimulus type and modality and the fact that crossmodal interactions are similar to within-modality effects support the idea that semantic knowledge resides in a distributed cerebral network, accessible from multiple input forms. More specifically, the scalp N400 seems to reflect a set of temporally restricted neural processes that are common to the analysis of all sensory inputs, allowing crossmodal interaction for the purposes of meaning construction.

However, the distribution across the scalp of the (functionally similar) observed negativity varies with stimulus type (see Ref. 53 for a more extensive discussion of the

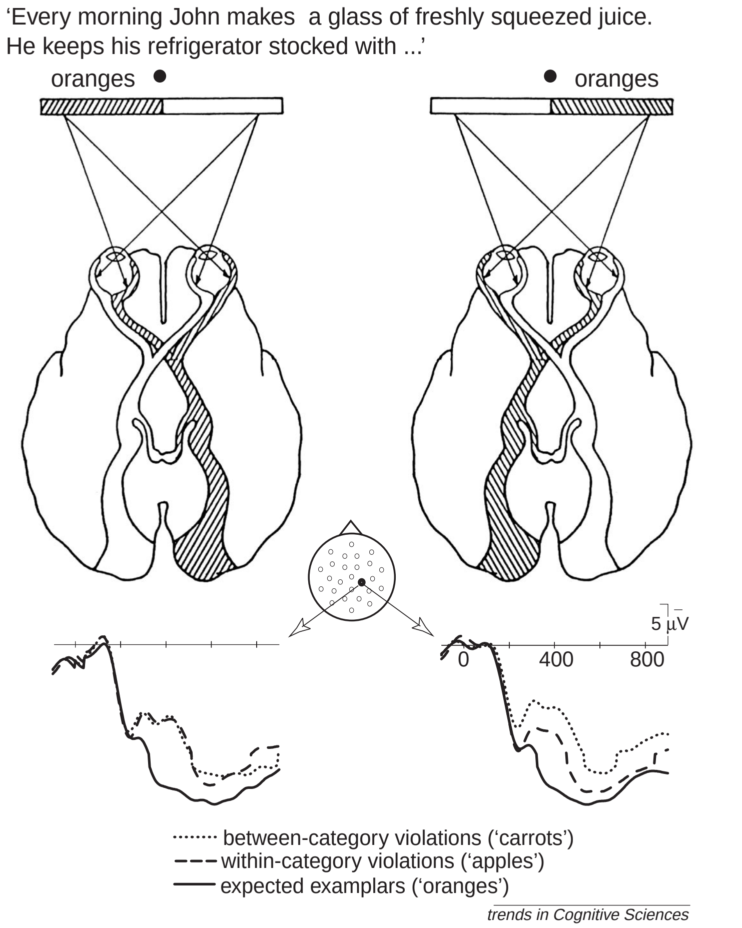

Fig. 4. Hemispheric differences in on-line semantic memory use. Eighteen participants read for comprehension the same sentences as described in Fig. 1 in a visual-half-field presentation design. Context words were presented at central fixation, whereas sentence-final target words (e.g. oranges) were presented with nearest edge two degrees to the left or right of fixation. As illustrated, words presented to the left visual field travel initially to the right hemisphere and vice versa. ERPs are shown here from a representative (right medial central) site as indicated. The response to target words presented to the right visual field (left hemisphere) (shown on right), yielded the same pattern as that observed with central fixation: expected exemplars (solid line) elicited smaller N400s than did violations of either type, but within-category violations (dashed line) also elicited smaller N400s than between-category violations (dotted line). This pattern is indicative of a 'predictive' strategy, in which semantic information associated with the expected item is pre-activated in the course of processing the context information. The response to targets presented to the left visual field (right hemisphere) (shown on left), however, was qualitatively different: expected exemplars again elicited smaller N400s than violations, but the response to the two types of violations did not differ. This pattern is more consistent with a plausibility-based integrative strategy. Taken together, the results indicate that the hemispheres differ in how they use context to access information from semantic memory during on-line language processing.

measurement and interpretation of scalp distribution information). The auditory N400, for example, is more evenly distributed over the scalp than the visual N400, which has a clear centro-parietal maximum[52]. Similarly, the negativity observed in response to pictures and to faces differs in distribution from that evoked by visual words[41,42,47], perhaps in part because of temporally overlapping negativities[44,47]. Such differences indicate that the neural generators for the effects seen with different types of stimuli are non-identical, which in turn implies that semantic knowledge might be not stored in a modality-independent manner. Indeed, there even seem to be distributional differences in the N400s evoked *within* a modality as a function of the type of semantic information elicited by the stimulus. For example, concrete words, that is words referring to pictureable objects, elicit N400s with a more anterior distribution, much like that seen to line drawings and photographs, than those elicited by abstract words[54], at least in the absence of strong contextual information[55]. In summary, the N400s elicited by different types of potentially meaningful stimuli are temporally coincident and seem to be functionally similar, but are likely to be anatomically non-identical.

Thus, the N400 data is consistent with neuropsychological data and results from other neuroimaging techniques[56–60] in suggesting that semantic memory may consist of featural mosaics distributed across multiple, higher-order perceptual and motor processing areas: the '*meow*' of a cat, for example, in auditory association cortex, the shape and color of a cat in extrastriate visual cortex, the 'furriness' of a cat in higher-order somatosensory areas, and so forth. The N400 data go further still, however, showing that meaning emerges from these distributed systems by virtue of temporally coincident and functionally similar activity within a number of brain areas. The semantic representation of a unified concept, then, would involve a distinct pattern of activation, in the N400 time window, across multiple brain areas, reflecting the contribution of each – for example, more visual for concrete words and pictures, more auditory for environmental sounds – plus activation in multimodal processing areas that would serve to 'bind' this distributed information together. Such a view is, in fact, supported by intracranial recording studies, which suggest that the scalp-recorded N400 is associated with waves of activity across multiple brain areas, including the inferotemporal cortex and superior temporal sulcus (which are implicated in higher-order, modality-specific perceptual processing), as well as the medial temporal lobe, hippocampus and ventrolateral prefrontal cortex (which process input from multiple modalities)[21,22,24,25]. The scalp-recorded N400, then, seems to be the reflection of coordinated activity in multiple brain areas during the retrieval of information from semantic memory in a variety of tasks and in response to various types of stimuli.

Conclusion

In summary, examination of the N400 has offered insights into meaning processing at various levels. It suggests that meaning is not an amodal, invariant, immutable representation in a brain area that can easily be localized or lesioned, but instead a polymodal, context-sensitive, constructive, spatially distributed and temporally extended process. ERP research reveals that the neural representations necessary for meaning to emerge carry their colors with them in what features they represent and how they are organized or both, and that this organization impacts how people make sense of the world, including linguistic inputs. More specifically, N400 results show that semantic information accrues gradually and continuously throughout the processing of a sentence, discourse, or even a list of words. This information serves not only to constrain, but in some cases to pre-activate, the perceptual and semantic features of forthcoming items, such that information congruent with the context or the predictions it has engendered is subsequently easier to assimilate and process. This ease of processing, in turn, seems to be manifested electrophysiologically as a reduction in N400 amplitude. Although we still have much to learn about the precise nature of the neural and computational processes underlying the N400, it seems clear that they arise from a distributed cortical network involved in meaning construction. No single brain site of meaning exists. The N400, however, is a sensitive index of semantic processes at a psychological level, which reflects the activity of a spatially distributed but temporally interlinked set of brain areas in both hemispheres (each of which makes a distinct contribution), whose function is to bridge modality-specific sensory information and integrated, conceptual-level representations. In short, the N400 provides a window into the neurobiology of meaning.

Acknowledgements

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Outstanding questions

- Does the scalp negativity between 200–500 ms post-stimulus-onset reflect: (1) a functionally and anatomically singular N400; (2) a family of functionally equivalent but anatomically distributed N400s; or (3) a set of functionally and anatomically distinct N400s?
- What is the mapping between psychological and neural notions of features, and what cognitive/neural principles (e.g. association, similarity, analogy) guide their functional organization as manifested in what we commonly refer to as semantic memory?
- How flexible is the organization of semantic memory in the face of experience and on-line contextual/environmental cues?
- To what extent and how are perceptual and semantic information shared across the two hemispheres during language processing?
- How do the two cerebral hemispheres coordinate their contributions to language processing in real time?
- How much, and which aspects, of perception are available for semantic processing?

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Extending the classical view of representation

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Representation has always been a central part of models in cognitive science, but this idea has come under attack. Researchers advocating the alternative approaches of perceptual symbol systems, situated action, embodied cognition, and dynamical systems have argued against central assumptions of the classical representational approach to mind. We review the core assumptions of the representational view and these four suggested alternatives. We argue that representation should remain a core part of cognitive science, but that the insights from these alternative approaches must be incorporated into models of cognitive processing.

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There is revolution in the air in cognitive science. Since the late 1950s, models of cognition have been dominated by representational approaches. These models posit some kind of internal mechanism for storing and manipulating data as well as processes that act on representations to carry out intelligent behaviors[1–3].

Although the field of cognitive science has made great strides, the early predictions that we would soon have autonomous robots and intelligent computers on our desktops have not yet come to pass. Researchers from a variety of perspectives have suggested that the standard representational assumptions made by cognitive models are to blame for this lack of progress. The suggested remedies range from additional information that should be included in representations to replacement of the dominant paradigm with an alternative.

This article sketches the classical view of representation that is widely employed in cognitive models. Then, four recent approaches to cognitive modeling are examined: perceptual symbol systems, situated action, embodied cognition, and dynamical systems. Each approach has been put forward as a successor to the classical view. We suggest that each of the four alternative approaches has something important to offer, but cannot replace the classical view. We end with a discussion of ways to reconcile the classical view with these alternatives.

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