Review

Event-related brain potentials and human language

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The human capacity to produce and comprehend language is one of the most distinctive characteristics of our species. However, understanding the cognitive and neural underpinnings of human language has proved difficult, in part because these processes are rapid, complex and (for the most part) inaccessible to conscious reflection. Methodologies are needed that provide continuous measurement during language processing and that do not rely on a conscious response. One such method involves the recording of event-related brain potentials (ERPs) elicited during language comprehension or production. ERPs are continuous, multidimensional records of the electrical activity that occurs in the brain during the process of interest. We review recent work demonstrating that ERPs are quite sensitive to (at least some of) the psychological and neural events underlying human language. Indeed, researchers have used ERPs to investigate the separability of syntactic and semantic processes, the on-line analysis of sentence constituent structure and the lexical processing capacities of language-disordered populations.

From a very young age, almost all humans can produce and comprehend language, seemingly with little effort. Understanding how humans accomplish these feats has proved considerably more difficult. The difficulty, in part, stems from the properties of language itself. The psychological processes underlying human language occur with great speed. Despite their rapidity, these processes are not instantaneous but instead are distributed over time. Furthermore, these processes are, by most accounts, highly complex and involve multiple levels of analysis (phonological, syntactic, semantic, etc.). By some means, the results of these analyses are then rapidly integrated into a coherent production or interpretation. Finally, these processes remain largely inaccessible to conscious reflection.

These qualities of human language pose a formidable methodological challenge. One might surmise that the ideal method for studying human language would mirror the properties of language itself. The ideal method should provide continuous measurement during the process of interest, be differentially sensitive to events occurring at distinct levels of analysis and not rely on conscious judgements. One method that approximates the ideal method is the recording of event-related brain potentials (ERPs) elicited during language processing[1]. ERPs are scalp-recorded changes in electrical activity that occur in response to a sensory, cognitive or motor event (Fig. 1). Topographical features of the ERP are referred to as components and can be described in terms of polarity (positive or negative), amplitude, onset, peak latency and scalp distribution. ERPs provide a millisecond-by-millisecond record of the electrical activity that occurs in the brain during the process of interest. ERPs are multidimensional (varying in polarity, latency, amplitude and scalp distribution). ERPs can be recorded without the subject having to make a conscious judgement. ERPs also offer the prospect of tying cognitive models of language processing more closely to their biological substrates.

However, these advantages are irrelevant unless ERPs prove to be sensitive to the psychological and neural processes underlying human language. In this review we will discuss (selectively) evidence that ERPs are quite sensitive to certain language-related processes. We also hope to illustrate, by way of example, how ERPs can be used to illuminate the psychological and neural underpinnings of human language.

Language comprehension

Phoneme perception

Human adults and infants perceive speech sounds categorically; that is, they are more sensitive to differences between speech sounds that cross phonetic category boundaries than to differences that do not[2]. Furthermore, newborns are sensitive to most phonetic distinctions, including distinctions that are not present in their native language[2]. This apparently innate propensity for categorical perception is augmented and altered by linguistic experience. By six months of age, infants form 'prototypes' of each category of speech sound in their native language[3]. These prototypes are thought

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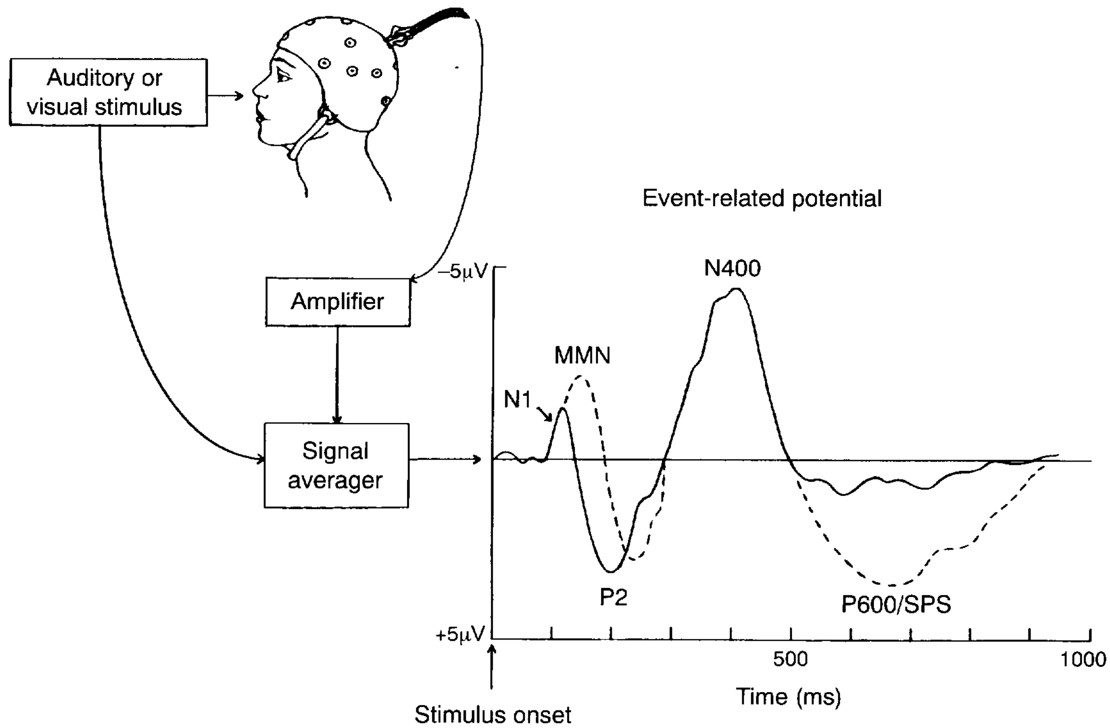

Fig. 1 Obtaining event-related brain potentials. Idealized waveform of the computer-averaged event-related potential to a visually or auditorally presented word. The ERP is not recognizable in the raw electroencephalogram (EEG) and is extracted from the EEG by averaging over many presentations of phonemes or words from the same stimulus category. ERP components that are observed typically under such conditions include the 'vertex potential' waves (N1 and P2), the mismatch negativity (MMN) and task-related 'endogenous' components (N400 and late positive shift). The mismatch negativity is elicited by auditory stimuli that are physically deviant from preceding stimuli. Endogenous components are influenced primarily by the cognitive, rather than the physical, aspects of the stimulus. The amplitude of the N400 component is affected by the semantic relationship between the target word and the preceding context, with semantically anomalous stimuli eliciting large-amplitude N400s. The P600/syntactic positive shift (SPS) is elicited by syntactically anomalous words.

to underlie a reorganization of phonetic category boundaries, in which the perceptual system becomes tuned specifically to the native language phonetic distinctions and loses sensitivity to non-native contrasts[3].

Recent research has shown that ERPs are sensitive to the categorical and prototypical aspects of phoneme perception. This research has taken advantage of mismatch negativity (MMN), a negative-going effect thought to reflect automatic, pre-attentive processes that respond to changes in the physical characteristics of auditory stimuli[4]. Researchers have presented a series of identical 'standard' speech sounds randomly intermixed with infrequent 'deviant' speech sounds that systematically differ from the standard stimulus. At least under certain experimental conditions, deviant stimuli that cross a phonetic category boundary (relative to the standard stimulus) elicit a robust MMN, whereas deviants from the same phonetic category as the standard do not[5]. Furthermore, a larger MMN is elicited when the deviant is a category prototype than when the deviant is a nonprototype[6]. Importantly, the neural generator of at least some of these MMN effects is in or near the left-hemisphere auditory cortex[6]. One reasonable interpretation of these findings is that phonemic codes are represented neurally in sensory memory (perhaps in the auditory cortex) and can serve as a basis for auditory mismatch detection[5,6]. This conclusion is consistent with the observation that aphasics suffering from left posterior lesions (near or including the left auditory cortex) show the MMN response to deviant non-linguistic stimuli but not to deviant speech stimuli[7].

Syntax and semantics

Perhaps the most fundamental distinction made by linguists is the one between syntax (sentence form) and semantics (sentence meaning). To most linguists, sentences that violate syntactic constraints (such as: 'John slept *the bed*') are clearly distinct from sentences that violate semantic constraints (such as: 'John spread his bread with *socks*'). Whether or not this distinction characterizes accurately the processes underlying language processing has been a matter of debate. Some psycholinguistic models posit separable processes that construct distinct syntactic and semantic representations of a sentence[8], whereas others do not[9].

Given their multidimensional qualities, ERPs might be an efficacious measure for examining this issue. Assuming that cognitively distinct processes are mediated by neurally distinct brain systems, evidence that syntactic and semantic phenomena elicit distinct patterns of brain activity could be construed to support the claim that separable syntactic and semantic processes exist. The pioneering work of Kutas and Hillyard demonstrated that semantically inappropriate words (such as 'socks' in the example above) elicit an increase in the amplitude of the N400 component, a negative-going wave that peaks at about 400 ms (Ref. 10) (see Box 1 and Fig. 2A). Subsequent research has shown that N400 amplitude is an inverse function of the semantic congruence between the target word and prior context, even when the target word is not semantically anomalous[11].

Researchers investigating the ERP response to syntactic anomalies have reported a variety of effects[12–21]. Critically,

Box 1. Phenomena that elicit the N400 and P600/SPS effects

N400 effect

Semantically or pragmatically inappropriate words:

'I take my coffee with cream and *dog*'.

'Those small spiders often *burn* new webs'.

False statements of category relationships:

'A hammer is a *bird*'.

Information that is inconsistent with prior knowledge:

'John is not a *lawyer*' (after having learned that John is in fact a lawyer).

P600/SPS effect

Phrase structure anomalies:

'The scientist criticized Max's *of* proof the theorem'.

Verb subcategorization anomalies:

'The broker persuaded *to* sell the stock'.

Sentence-constituent movement anomalies:

'I wonder which dress the guests at the party were shocked *when* the bride wore'.

Verb tense anomalies:

'The cats won't *eating* the food that Mary leaves them'.

Subject-verb number disagreement:

'The elected officials *hopes* to succeed'.

Reflexive-antecedent number disagreement:

'The hungry guests helped *himself* to the meal'.

Reflexive-antecedent gender disagreement:

'The successful woman congratulated *himself* on the promotion'.

however, none of these effects resembles the centroparietally distributed N400 effect. At least under certain experimental conditions, a disparate set of syntactic anomalies elicits a large-amplitude, centroparietal positive wave in the ERP, variously labeled the P600 effect and the syntactic positive shift (SPS; see Box 1 and Fig. 2B)[12–19]. In most reports, the P600 effect begins about 500 ms after presentation of the anomalous word and persists for several hundred milliseconds. P600 amplitude is an inverse function of the syntactic congruence between the target word and preceding sentence material[17]. Importantly, words that are both semantically and syntactically anomalous elicit both the N400 effect and the P600 effect within the same epoch of activity (Fig. 2C)[19]. Other ERP responses to syntactic anomalies have been reported. For example, sometimes syntactic anomalies elicit a negative-going wave between 200 and 500 ms over anterior portions of the left hemisphere[20,21].

The observation that the brain responds differently to syntactic and semantic anomalies is consistent with the claim that separable syntactic and semantic processes exist. Neville and colleagues reached a similar conclusion based on different evidence[22]. These researchers contrasted the ERP response to function words (such as articles and prepositions) and content words (such as nouns and verbs). In English, the distinction between function and content words parallels the distinction between syntax and semantics: function words are agents of phrasal construction, whereas content words convey meaning. Neville and colleagues reported that function and content words (when presented in grammatical, coherent sentences) elicited distinct ERPs in normal subjects. Function words elicited a

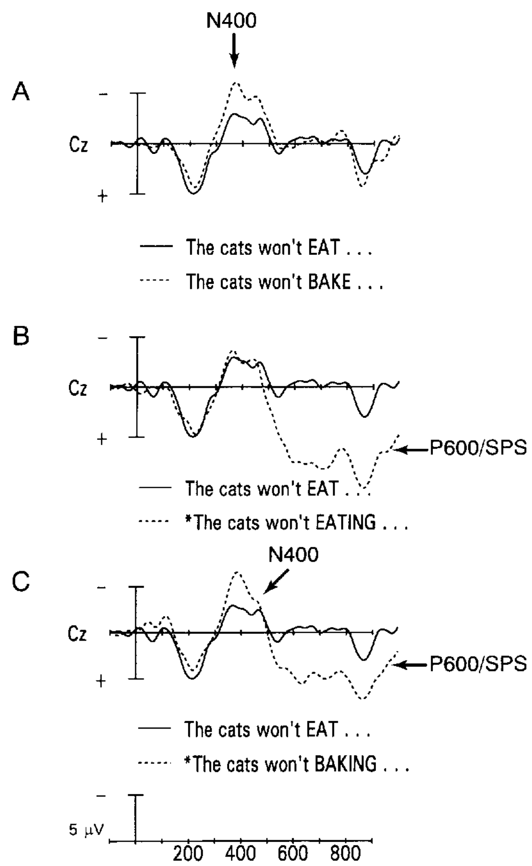

Fig. 2 Event-related brain potentials (ERPs) elicited by linguistically anomalous words encountered during sentence comprehension. Normal reading rates and connected natural speech introduce the problem of component overlap, in which ERPs elicited by the word of interest are contaminated by the ERPs to subsequent words. For this reason, the standard method has involved the visual presentation of sentences in a word-by-word manner, with typical word-onset asynchronies ranging from 300 to 1000 ms. (For a review of a study involving continuous natural speech stimuli, see Ref. 16.) In the experiment described here (and in subsequent figures, unless specified otherwise) sentences were presented visually with a 650 ms interval between word onsets, and each waveform reflects activity averaged over 12–18 subjects and 30–40 trials. Further, subjects were asked to perform a sentence-acceptability judgement at the end of each sentence (for studies in which subjects have performed no task other than comprehension, see Refs 13 and 18). **(A)** ERPs (recorded over the vertex site Cz) to non-anomalous words (such as: 'The cats won't *eat* the food...') and semantically anomalous words (such as: 'The cats won't *bake* the food...'). The semantically anomalous words elicit an N400 component with increased amplitude relative to the N400 elicited by the non-anomalous words. **(B)** ERPs to non-anomalous and syntactically anomalous verb tense violations (such as: 'The cats won't *eating* the food...'). The syntactically anomalous words elicit a late positive shift (P600) beginning at about 500 ms, relative to ERPs elicited by the non-anomalous words. **(C)** ERPs to non-anomalous and doubly anomalous words that are both semantically and syntactically anomalous (such as: 'The cats won't *baking* the food...'). Note the biphasic response [increase in N400 amplitude followed by a late positive shift (P600)] to the doubly anomalous words relative to the ERPs elicited by non-anomalous words. Negative voltage is plotted up. Each hashmark represents 100 ms. The vertical calibration bar represents 5 μV. An asterisk at the beginning of a sentence indicates ungrammaticality (based on Ref. 19).

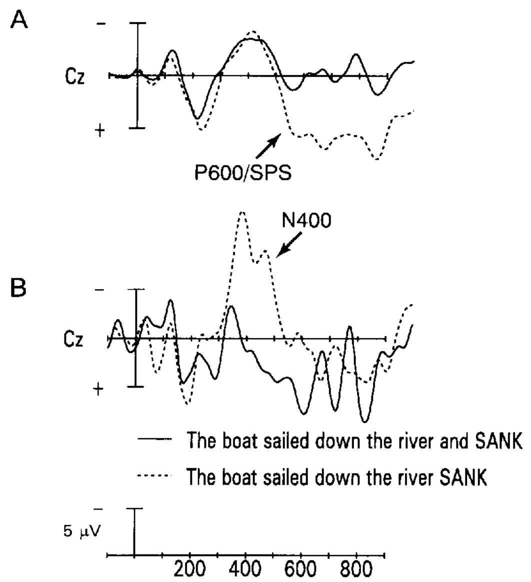

Fig. 3 Individual differences in sentence parsing as revealed by event-related brain potentials (ERPs). ERPs (recorded over site Cz) to the syntactically disambiguating word in sentences such as: 'The boat sailed down the river *sank* during the storm' and to the same word in unambiguous sentences. **(A)** ERPs averaged over 11 subjects who exhibited a P600 response to the critical words. **(B)** ERPs averaged over three subjects who exhibited an N400 response to the critical words (based on Ref. 24).

negative component peaking at 280 ms over anterior regions of the left hemisphere (N280), whereas content words elicited a posterior N400. One hypothesis is that the N280 reflects the grammatical work performed by function words. If so, one would expect the N280 to be reduced or absent in populations that lack grammatical competence. And indeed, deaf subjects who had not fully acquired English grammar showed a normal N400 response to content words but did not show an N280 response to function words[22].

Sentence comprehension

Given that syntactic analysis seems to be a part of language comprehension, the question of exactly how the reader determines the syntactic structure of a sentence becomes a central concern. Researchers have examined this question by presenting sentences containing a syntactic ambiguity, that is, a situation in which more than one well-formed syntactic analysis can be assigned to a string of words. Usually, subsequent words indicate the correct analysis. For example, in the sentence: 'The lawyer charged *the defendant* was lying', the grammatical role of the noun phrase 'the defendant' is temporarily ambiguous between an 'object of the verb' role and a 'subject of an upcoming clause' role. The fact that the subject role is appropriate becomes clear only after encountering the disambiguating auxiliary verb 'was'. Current theories predict that in such situations the reader will assign the object role to 'the defendant'[8]. This decision will result in a processing problem when the auxiliary verb is encountered; under the object analysis, the auxiliary cannot be attached to the preceding sentence material. Consequently, this theory predicts that readers should (at least momentarily) perceive the auxiliary verb to be syntactically anomalous. Consistent with this prediction, auxiliaries in such sentences elicit a P600-like positive shift[17]. One interpretation of these results is that readers commit themselves to a single syntactic analysis when confronted with a syntactic ambiguity, rather than building all possible structures in parallel or waiting until disambiguating information indicates which analysis is correct before assigning grammatical roles to words.

ERPs can also reveal the effects of semantic context, manifested as changes in N400 amplitude. For example, words occurring in later positions within a sentence elicit smaller N400s than do words occurring early in the sentence. That is, as contextual constraints increase (simply through the addition of words), N400s to words in the sentence decrease. Furthermore, this is specifically an effect of semantic context. These N400 modulations are not observed in grammatically constraining but nonsensical sentences (such as: 'They married their uranium in store and cigarettes')[23].

In the studies reviewed above, the distinction between syntactic and semantic phenomena was defined with reference to static theories of linguistic structure and linguistic processing. However, data from one recent study suggest that the processing strategies and linguistic competences that subjects bring with them may, in part, determine both the category that an event falls into and the brain response elicited by that event[24]. Subjects read sentences (such as: 'The boat sailed down the river *sank* during the storm') that were temporarily ambiguous between a relative clause analysis and a simple active analysis. The syntactically disambiguating word ('sank' in the example above) indicated that the relative clause analysis is correct. These sentences are almost universally misparsed as simple active structures; under a simple active analysis, the disambiguating word cannot be attached to the prior sentence material. As expected, most subjects exhibited a P600 effect to the disambiguating word (Fig. 3A). However, in a minority of subjects these words elicited a large N400 effect (Fig. 3B). Apparently, some subjects were sensitive to the syntactic ramifications of these anomalies (and thus exhibited the P600 effect), whereas other subjects were sensitive to the semantic ramifications (and thus exhibited the N400 effect). The existence of such individual differences raises some compelling theoretical questions. For example, do these differences among subjects reflect differences in linguistic processing or knowledge? What is the etiology underlying these differences? One possibility is that these individual differences reflect differences among subjects in working memory capacity. Recent work has linked variation in working memory capacity to individual differences in sentence processing[25]. In any case, these ERP results indicate quite clearly the existence of individual differences in the processing response to complex sentences.

Are these language-sensitive effects uniquely linguistic?

One of the standard doctrines within modern neuropsychology is the existence of neural systems that are dedicated to language processing. Therefore, one can ask whether these language-sensitive ERP effects are language specific. Although this question is difficult to address directly, researchers have investigated a salient alternative possibility with respect to the P600 effect: namely, that the P600 is a longer-latency manifestation of the domain-general P300 family of components. The P300 is elicited by task-relevant, unexpected events[26,27]. P300 amplitude is a function of the degree of deviance between the properties of the target stimulus and the preceding stimuli[27].

The distinctiveness of two brain responses can be assessed in several ways. Firstly, the similarity of the underlying neural events can be estimated by comparing the scalp distributions of the components. Components with distinct distributions are generated by non-identical brain systems[27]. Secondly, one can determine whether stimulus and task manipulations affect the components of interest similarly. If so, then probably the components are related functionally. Thirdly, one can determine whether the components have additive effects. This approach follows from Helmholtz's Principle of Superposition, which maintains that electrical fields propagating through a conductive medium summate where they intersect. Evidence of additivity implies independence of the underlying neural sources. One recent study has shown that the P300 and P600 have reliably different scalp distributions, respond differentially to manipulations of stimuli and task and have additive effects when a doubly anomalous word (one expected to elicit both the P300 and P600) is presented (Fig. 4)[28]. Thus, the P600 might be (at least to an interesting degree) distinct, both neurally and functionally, from the P300 family of components. Of course, such evidence does not imply necessarily that the P600 is in any sense a direct manifestation of linguistic processes.

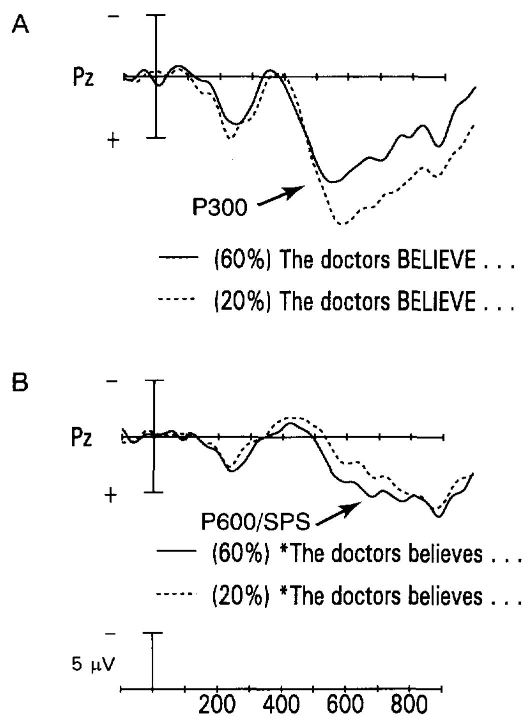

Fig. 4 Sensitivity of P300 and P600 components to manipulations of stimulus probability. One means for determining whether two event-related brain potential (ERP) components are functionally distinct is to determine whether the components respond similarly to stimulus manipulations. P300 amplitude is an inverse function of the probability of the eliciting event. The question of interest is whether P600 amplitude is similarly sensitive. Critical stimuli in this experiment were sentences containing either a word in uppercase letters (the type of 'physical' anomaly known to elicit the P300 response) or a verb that disagreed with the subject noun in number (a syntactic anomaly known to elicit the P600 response; see Ref. 18). The percentage of trials in which subjects saw each type of anomaly was manipulated (20% vs 60%). **(A)** ERPs (recorded over site Pz) elicited by physically anomalous uppercase words that appeared in 20% or 60% of the sentence trials. **(B)** ERPs to syntactically anomalous words that appeared in 20% or 60% of the sentence trials. Probability had a reliable effect on the response to the physical anomalies but not on the response to syntactic anomalies. Although the positive wave elicited by uppercase words peaked later than 300 ms, this effect was highly similar to P300s reported previously. P300 latency is known to be a function of stimulus complexity (based on Ref. 28).

Language production

Due to the contaminating effects of the large-amplitude electromyographic activity associated with articulation, the electroencephalogram (EEG) associated with speech planning and production is difficult to measure directly. Nonetheless, clever designs allow one to study production processes using ERPs. One such study took advantage of the lateralized readiness potential (LRP), a potential that develops in the period just prior to a motor response[1]. LRP amplitude is largest over motor cortex contralateral to the responding hand. Prior work has shown that the LRP is an index of response preparation and that it can be elicited even in situations where the prepared response is never performed[29]. Such a scenario can arise when partial information (available early) leads the subject to prepare a response but full information (available later) indicates that the response should not be made.

Researchers used the LRP to test a basic claim of current speech production models, namely, that the semantic properties of to-be-spoken words are retrieved first, followed by the phonological forms[30]. Subjects performed two tasks simultaneously: a picture-naming task (to initiate speech production processes) and a 'go/no-go' response task involving semantic and phonological judgements about the picture stimulus. On 'go' trials, subjects pressed a button with their left or right hand, whereas on 'no-go' trials subjects did not make a response. The semantic judgement involved deciding whether the pictured object was animate, whereas the phonological judgement involved determining whether the picture name ended with the phoneme /s/. On some trials, the semantic information determined the hand for the response and the phonological information determined whether the response was made (go trial) or not (no-go trial). On other trials, the contingencies were reversed. If semantic information is available earlier than phonological information, then an LRP should develop on no-go trials in which semantic information determined the response hand and phonological information determined whether the response should be made. This prediction follows because subjects would prepare a response based on the semantic information (available early) before accessing the phonological information (available later) indicating that no response should be made. Conversely, no LRP should develop when the contingencies are reversed; the semantic information (available early) should inform the system not to prepare a response. Exactly this result was observed, suggesting that the speech planning system does indeed have access to semantic information before it has access to phonological information.

Language dysfunction

ERPs reflect the summed, simultaneously occurring, post-synaptic activity of large groups of neurons in the brain. This fact, combined with the advantages outlined above, would seem to make ERPs ideal tools for examining language dysfunctions (such as aphasias and dyslexias) that result from disturbances to the biological systems underlying language. A good example is provided by recent studies investigating the lexical-semantic processing capabilities of Broca's aphasics[31,32]. Broca's aphasics and matched controls were presented with two sets of stimuli: pairs of spoken words (some of which were semantically related) and spoken sentences that ended in a semantically congruous or anomalous word. Both the aphasics and the normal controls showed a reduction in N400 amplitude to target words that were preceded by semantically related prime words. There were no reliable differences in the timing, amplitude or temporal course of this effect. In both populations, the sentence-final anomalous words elicited a large N400 effect, relative to the congruous words. However, the size of this effect was reduced in amplitude and delayed in onset in the aphasic subjects relative to the normal subjects. One interpretation is that although Broca's aphasics can access lexical-semantic information in a normal manner (as reflected in normal word-association effects in the word pair task), they are impaired in their ability to integrate this information into a representation of the overall context (as reflected in the sentence comprehension task). Most importantly, these studies demonstrate that it is possible to record language-related ERP effects in aphasic populations.

Conclusions

ERPs are demonstrably sensitive to at least a subset of the psychological and neural events underlying human language. Furthermore, this sensitivity can be exploited to investigate the real-time comprehension and production of language, both in normal and disordered populations. ERP research not reviewed here has investigated such disparate phenomena as the effects of abnormal language exposure on neural organization[33], bilingualism[34], working memory and language processing[35] and linguistically encoded social stereotypes[36]. Progress is also being made in locating the neural source of certain language-sensitive ERP effects (such as the N400)[37]. Nonetheless, many language phenomena might prove unamenable to ERP investigations. ERPs represent brain activity averaged over both items and subjects, usually time-locked to the onset of a stimulus. The most observable processes are those that have an invariant temporal relation to the onset of a stimulus (such as word processing and syntactic analysis). Processes that are not linked reliably to stimulus onset will be less observable.

Finally, we know little about the cognitive and neural processes made manifest by these language-sensitive ERP effects. In particular, we do not know whether these effects reflect linguistic processes directly or, instead, reflect processes that are correlated with but indeterminately removed from the linguistic processes themselves. One might hope that by learning more about the underlying processes (both cognitive and neurological), ERPs will become increasingly useful as tools for studying human language and for tying cognitive models of language processing more closely to their biological substrates.

Outstanding questions

- What are the precise cognitive events underlying the language-sensitive ERP effects? To what extent do the functional categories posited by psycholinguistic processing theories map on to the physiological variables reflected in the ERP? Given that most theories hold that syntactic analysis precedes semantic analysis, why does the N400 effect (which is sensitive to semantic variables) temporally precede the P600 effect (which is sensitive to syntactic variables)?
- Will the results reported here (obtained in English and related European languages) generalize to languages that are structurally different, for example, highly case-marked languages such as Swahili?
- How do these ERP effects develop during the acquisition of language? Can these effects be used to investigate first- and second-language acquisition?
- What factors underlie the individual differences observed recently in the ERP correlates of sentence comprehension?
- How far down the 'path of comprehension' will ERPs take us? Given that ERPs reflect brain activity averaged over items and subjects, it seems likely that only those neural events that are time-locked closely (and reliably) to the onset of a stimulus across trials and subjects will be observable. Which language-related events have the necessary temporal qualities, and which do not?

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Computational approaches to motor control

Daniel M. Wolpert

This review will focus on four areas of motor control which have recently been enriched both by neural network and control system models: motor planning, motor prediction, state estimation and motor learning. We will review the computational foundations of each of these concepts and present specific models which have been tested by psychophysical experiments. We will cover the topics of optimal control for motor planning, forward models for motor prediction, observer models of state estimation and modular decomposition in motor learning. The aim of this review is to demonstrate how computational approaches, as well as proposing specific models, provide a theoretical framework to formalize the issues in motor control.

This review will focus on several basic theoretical issues in motor control as well as supporting experimental studies. While many of the concepts discussed are applicable to all areas of motor control, including eye movements, speech production and posture, we will focus on arm movements as an illustrative system. From an engineering perspective the arm can be considered as a system whose inputs are the motor commands emanating from the controller within the central nervous system (see Fig. 1). In order to determine the behaviour of the arm in response to this input an additional set of variables, called state variables, must also be known. For example, in a robotic model of the arm the motor command signals the torques generated around the joints and the state variables could be the joint angles and

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