Brain responses to nouns, verbs and class-ambiguous words in context

Kara D. Federmeier,¹ Jessica B. Segal,³ Tania Lombrozo⁴ and Marta Kutas^{1,2}

Departments of ¹Cognitive Science and ²Neurosciences, University of California San Diego, La Jolla, California, ³Department of Neurology, Johns Hopkins University, Baltimore, Maryland and ⁴Stanford University, Stanford, California, USA Correspondence to: Kara D. Federmeier, Department of Cognitive Science, University of California, San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0515, USA E-mail: kfederme@cogsci.ucsd.edu

Summary

Recent neuropsychological and imaging data have implicated different brain networks in the processing of different word classes, nouns being linked primarily to posterior, visual object-processing regions and verbs to frontal, motor-processing areas. However, as most of these studies have examined words in isolation, the consequences of such anatomically based representational differences, if any, for the processing of these items in sentences remains unclear. Additionally, in some languages many words (e.g. 'drink') are class-ambiguous, i.e. they can play either role depending on context, and it is not yet known how the brain stores and uses information associated with such lexical items in context. We examined these issues by recording event-related potentials (ERPs) in response to unambiguous nouns (e.g. 'beer'), unambiguous verbs (e.g. 'eat'), class-ambiguous words and pseudowords used as nouns or verbs within two types of minimally contrastive sentence contexts: noun-predicting (e.g. 'John wanted THE [target] but ...') and verb-predicting ('John wanted TO [target] but ...'). Our results indicate that the nature of neural processing for nouns and verbs is a function of both the type of stimulus and the role it is playing. Even when the context completely specifies their role, word class-ambiguous

items differ from unambiguous ones over frontal regions by ~150 ms. Moreover, whereas pseudowords elicit larger N400s when used as verbs than when used as nouns. unambiguous nouns and ambiguous words used as nouns elicit more frontocentral negativity than unambiguous verbs and ambiguous words used as verbs, respectively. Additionally, unambiguous verbs elicit a left-lateralized, anterior positivity (~200 ms) not observed for any other stimulus type, though only when these items are used appropriately as verbs (i.e. in verb-predicting contexts). In summary, the pattern of neural activity observed in response to lexical items depends on their general probability of being a verb or a noun and on the particular role they are playing in any given sentence. This implicates more than a simple two-way distinction of the brain networks involved in their storage and processing. Experience, as well as context during on-line language processing, clearly shapes the neural representations of nouns and verbs, such that there is no single neural marker of word class. Our results further suggest that the presence and nature of the word class-based dissociations observed after brain damage are similarly likely to be a function of both the type of stimulus and the context in which it occurs, and thus must be assessed accordingly.

Keywords: language; sentence processing; word class; ambiguity; ERPs

Abbreviations: ANOVA = analysis of variance; ERP = event-related potential

Introduction

Lexical items are divided into different word classes, such as nouns and verbs, because they play different semantic and syntactic roles in language and, in behavioural tasks, are responded to differentially by language users. For example, whereas nouns are pointers to objects (people, places and things), verbs generally refer to actions and states. Verbs have been described as more 'relational' in their semantics than nouns (e.g. Gentner, 1981; Langacker, 1987). Furthermore, at least in English, nouns tend to be more narrowly defined than verbs, and there are larger numbers of low-frequency noun than verb tokens (Gentner, 1981). In any given language, nouns and verbs typically receive different types of inflectional (grammatical) markings and/or appear in different canonical places in the sentence structure (for a discussion of the importance of such grammatical markings in unifying the verb class in particular, see e.g. Maratsos, 1990). Perhaps because of these semantic and syntactic differences, nouns are acquired earlier during language development (e.g. Nelson, 1973) and are remembered more easily than verbs (e.g. Wearing, 1973; Thios, 1975; Reynolds and Flagg, 1976); nouns are also less likely than verbs to be altered during within-language paraphrasing or across-language translation (Gentner, 1981).

Of long-standing interest is the question of whether there is a neural representational counterpart to the linguistically and psychologically defined distinction between nouns and verbs. Neuropsychological evidence for double dissociation in performance in noun- and verb-production tasks has suggested that this may be the case (e.g. Miceli et al., 1988; Caramazza and Hillis, 1991). Whereas left, anterior damage has been linked to difficulty in the production of action verbs, difficulty in naming objects has been reported to follow left temporal damage (Damasio and Tranel, 1993; Daniele et al., 1994). This dissociation has led to the hypothesis that noun retrieval and verb retrieval may be mediated by different neural networks: a frontal network built in part from motorprocessing regions involved in the retrieval of words for actions (verbs), and a posterior network built in part from visual object-processing regions involved in the retrieval of words for objects (nouns) (e.g. Damasio and Tranel, 1993; Pulvermüller, 1999). However, evidence for this neural dissociation has come primarily from observations of impaired confrontation naming and has been restricted to concrete nouns and action verbs. [Daniele and colleagues also reported comprehension deficits in their patients (Danielle et al., 1994).] It thus remains unclear whether these patients' deficits are specific to production or involve lexical representation more generally, and whether the relevant dimension is actually word class (noun, verb) or specifically actions versus concrete objects.

In fact, finding clear evidence for a comparable double dissociation as a function of word class in intact individuals has proved more elusive. For example, Martin and colleagues found substantial overlap in PET activations during the generation of colour terms and action verbs (Martin et al., 1995). Moreover, the only area of activation specific to action naming was located in the left middle temporal lobe, not in the frontal cortex. Another study, comparing noun and verb generation more generally (participants generated verbs in response to a noun prompt or nouns in response to a superordinate category label prompt), reported no differences in activation patterns as a function of word class (Warburton et al., 1996). Finally, a PET study examining noun and verb comprehension using a lexical decision task described areas in the dorsolateral frontal cortex and lateral temporal cortex that were more responsive to verbs than nouns, but no areas that showed a preferential response to nouns (Perani et al., 1999). These differences did not interact with concreteness, suggesting that they were representative of the lexical class as a whole. The verb-specific activations were hypothesized to reflect the richer structural/syntactic information associated with verbs; the authors also suggest that their failure to find a double dissociation may indicate that the neuropsychological results reflect more about the semantic properties of actions and objects in particular than about nouns and verbs per se.

Electrophysiological studies of noun and verb processing have yielded similarly mixed results. In a semantic categorization task, Dehaene found a left, inferior frontal event-related potential (ERP) positivity beginning ~250 ms after stimulus onset that was specific to action verbs (as opposed to animal names and proper names) (Dehaene, 1995). Comparing German action verbs and concrete nouns using a lexical decision task, Pulvermüller and colleagues also reported ERP differences over frontal and central electrode sites beginning ~200 ms after stimulus onset (Preissl et al., 1995). They observed increased frontal positivity ('P200') in the ERP in response to verbs relative to nouns, and linked the effect to the different motor associations afforded by nouns and verbs, according to their norming results. There have also been reports of word class-related differences in EEG gamma band activity 500-800 ms after stimulus onset (Pulvermüller et al., 1996, 1999a), verbs showing greater activity over central ('motor') sites and nouns showing greater activity over posterior ('visual') sites. However, for all these studies there remains the question of whether differences hold for nouns and verbs as a class. Pulvermüller and colleagues have suggested that their observations reflect semantic (motor or visual) associations as opposed to word class (Pulvermüller et al., 1999b), as they found topographical differences within the noun class as a function of motor associations and failed to find differences between action verbs and nouns that scored high on action associations. (Note, however, that it is difficult to compare these results with other reports of noun/verb differences, because no waveforms are presented in the paper.)

Indeed, some researchers have failed to find differences between nouns and verbs when a broader range of items (including abstract nouns and non-action verbs) is used. In a semantic priming paradigm comparing noun-noun and nounverb pairs, Gomes and colleagues observed no word classrelated ERP topographic differences in either the visual or the auditory modality (though word class-related differences in N400 latency and effect size were observed) (Gomes et al., 1997). Gomes and colleagues interpret this difference as reflecting generally stronger lexical association among nouns than between nouns and verbs. Examining words extracted from a prose passage read for comprehension, Osterhout et al. and Brown et al. also failed to find distributional differences in the ERP response to nouns and verbs, though Brown and colleagues found overall increased negativity to verbs beginning at ~250 ms (Osterhout et al., 1997, in English; Brown et al., 1999, in Dutch). Osterhout and colleagues did observe slight differences in topography, however, when the same nouns and verbs were presented in scrambled prose, nouns showing a greater degree of rightlateralization in the N400 (Osterhout et al., 1997). However, as neither the study of Osterhout and colleagues nor that of Brown and colleagues was specifically designed to compare nouns and verbs, the two classes were not controlled for length, frequency, sentence position, etc.

In contrast, in an early series of studies, Brown and colleagues found consistent topographic differences in the ERP response to word class-ambiguous items (e.g. 'fire') when these were used as nouns versus verbs (Brown *et al.*, 1973, 1976, 1980). In both English and Swiss German, they observed that ambiguous items used as nouns ('sit by the fire') generated more positivity anteriorly and more negativity posteriorly in the first 300 ms than the same items when used as verbs ('ready, aim, fire'). They also observed a similar topographic difference in response to a degraded auditory signal (that could be recognized as speech but whose lexical content could not be identified) as a function of instructions to participants to imagine that it represented a phrase containing an ambiguous item used as either a noun or a verb.

Thus, there are suggestions of neural differences as a function of word class across a variety of paradigms and methods. These differences, however, have not been very consistent, and their meaning remains unclear for a number of reasons. First, the majority of studies, especially those that do find differences between nouns and verbs, have focused on a subset of each class, particularly action verbs and concrete nouns. Thus, it is not yet known which, if any, of the effects that emerge from these studies can be generalized to nouns and verbs as a more general class and which, instead, are specific to the semantic properties of the subset that has been studied. Secondly, the majority of studies have been done with isolated words and have employed tasks, such as lexical decision, that neither require nor encourage semantic or syntactic analysis of the target lexical items (which may tend to minimize the chance of observing word class-related differences). Finally, there is the issue of word class-ambiguous items. Whereas in some languages, such as German, lexical items are for the most part clearly either nouns or verbs, in other languages, such as English, there are large numbers of lexical items that can be used as both nouns and verbs, depending on the context. Such nounverb homophony has been shown to increase naming accuracy in some brain-damaged patients (e.g. Kemmerer and Tranel, 2000), whereas others have reported patients with deficits selective to one of the senses of such ambiguous words (e.g. Caramazza and Hillis, 1991). Most of the studies in normal individuals have not explicitly addressed this factor and differ in whether and, if so, to what extent ambiguous items were included in their materials. The possible distinction between word class-ambiguous and unambiguous items also remains largely unaddressed in theoretical proposals about the neural basis of word class representation, although it has played an important role in theories of lexical access.

Here, we describe an ERP study of noun and verb processing, taking these issues into consideration. We set out to compare specifically the brain's response to word classambiguous English words (e.g. 'drink') with that to their unambiguous noun and verb counterparts (e.g. 'beer', 'eat'), as well as with the response to pronounceable pseudowords with no pre-existing lexical representation (e.g. 'phream'). For both class-ambiguous and class-unambiguous items, we use words with a range of meanings, including concrete as well as abstract nouns and action as well as non-action (e.g. psychological state) verbs. We examined the responses to these three types of stimuli in minimally contrastive sentence contexts, one-half of which were compatible with a noun but not a verb in the target position (e.g. 'She liked the [target] . . .') and the other half of which were compatible with a verb but not a noun in the target position (e.g. 'She liked to [target] . . .').

By using both ambiguous and unambiguous items and by examining responses to nouns and verbs in context, we can ask whether the word class differences we observe, if any, arise from the way in which these items are represented or the way in which they are processed on-line, or both. Are there differences between lexical items that are unambiguously verbs and those that are unambiguously nouns that hold irrespective of the context in which these items appear? If so, we may conclude that these lexical items are probably represented differently in the brain. Do ambiguous items behave like their unambiguous counterparts when placed in disambiguating contexts, suggesting the possibility that there are multiple representations (i.e. one for the verb sense and one for the noun sense) of these items across different neural networks? Are there differences between items that are used as nouns and verbs in context regardless of whether these items are ambiguous or unambiguous in their word class out of context, or, indeed, regardless of whether these items have a pre-existing lexical representation? Such a finding would suggest that there are important word class differences that stem from the roles that nouns and verbs play in on-line language comprehension in addition to any differences in lexical representation per se.

Methods Material

Stimulus materials consisted of 60 each of four types of target words: (i) word class-ambiguous items that can be used as either nouns or verbs (e.g. hammer, drink, smoke, promise); (ii) unambiguous nouns (e.g. desk, beer, valley, truth); (iii) unambiguous verbs (e.g. eat, teach, grow, improve); and (4) pronounceable pseudowords, derived from word class-ambiguous items that were not used in the experiment [e.g. breat (heat), dight (fight), domp (romp), stive (drive)]. All pseudowords were in agreement with the phonological and orthographic rules of English. All stimuli were matched for length and real words were matched for word frequency (Francis and Kucera, 1982). In addition, word class-ambiguous items were controlled for their average frequency of use as nouns and verbs (such that, although the frequency of individual items was often biased towards the noun or verb sense, across the entire set of class-ambiguous items average noun-use and verb-use frequencies were equated).

Target words appeared in two types of minimally contrastive sentence contexts. Noun-predicting contexts consisted of a noun-phrase subject and a verb followed by 'the' (e.g. 'John wanted the . . .'), while verb-predicting contexts consisted of a noun-phrase subject and a verb followed by the infinitive marker 'to' (e.g. 'John wanted to . . .'). In all, 27 different lead-in verbs were used, all of which were compatible with either type of continuation [e.g. liked (to, the); planned (to, the); forgot (to, the); learned (to, the)]. Across the experiment, each target word appeared once in a noun-predicting context and once in the corresponding verb-predicting context; sentences were divided into two lists so that a given participant saw each target word only once. Sentences continued beyond the target word with a connector: the word immediately after the target and the total sentence length were matched across conditions. An example set of stimuli is given below:

He learned to joke and became the life of the party.

He learned the joke and repeated it incessantly.

Jim learned **to solution** but then wasn't allowed to use his calculator.

Jim learned **the solution** but went blank when it was time for the test.

The girl learned **to carve** but found it was more tedious than she had thought.

The girl learned **the carve** but hated working with the material. Cindy learned **to phream** from watching her grandfather at work. Cindy learned **the phream** from her ballroom dance professor.

In all, each participant read 240 experimental sentences along with 60 filler sentences (which described temporal relations between two events). Sentences were randomized once within each of the two lists and then presented in the same order for each participant.

Participants

Twenty-two undergraduates of the University of California San Diego (UCSD) (11 men and 11 women, age 18–27 years, mean age 21 years) participated in the experiment for cash and/or credit. Participants gave informed, written consent, and the study was approved by the UCSD Human Subjects Committee. All participants were right-handed, as assessed by the Edinburgh inventory (Oldfield, 1971), native English speakers with no history of reading difficulties or neurological/psychiatric disorders; eight of the volunteers reported having a left-handed or ambidextrous family member. Eleven participants were assigned randomly to each of the two stimulus lists.

Experimental procedure

Volunteers were tested in a single experimental session conducted in a soundproof, electrically shielded chamber. They were seated ~60 cm in front of a monitor screen and



Fig. 1 Electrode locations, shown with reference to the location of sites in the 10–20 system. The 26 electrode site locations are laid out to approximate the arrangement over the head as seen from the top (front of head at top of figure). Electrode MiPf corresponds exactly to Fpz in the 10–20 system, MiCe to Cz, MiPa to Pz, and MiOc to Oz. For the purposes of comparison, the other 10–20 locations are marked with filled circles.

instructed to read the experimental sentences for comprehension. The session began with a short practice trial designed to acclimatize the volunteers to the experimental conditions and task. The presentation of each sentence was preceded by a series of crosses to orient the participant towards the centre of the screen. The sentence was then presented one word at a time in the centre of the screen; each word was presented for a duration of 200 ms with a stimulus–onset asynchrony of 500 ms. Participants were asked not to blink or move their eyes during sentence presentation. The final word of each sentence was followed by a blank screen for 2500 ms, after which the next sentence or a comprehension probe sentence appeared automatically.

Comprehension probe sentences randomly followed onethird of the experimental sentences. These appeared in full on the screen. Volunteers pressed a button to indicate whether the probe sentence was an 'accurate restatement' of the immediately preceding experimental sentence. Assignment of response hand was balanced across subjects.

EEG recording parameters

The EEG was recorded from 26 geodesically spaced tin electrodes embedded in an Electro-cap (Fig. 1). These sites included midline prefrontal (MiPf), left and right medial prefrontal (LMPf and RMPf), left and right lateral prefrontal (LLPf and RLPf), left and right medial frontal (LMFr and RMFr), left and right mediolateral frontal (LDFr and RDFr),

left and right lateral frontal (LLFr and RLFr), midline central (MiCe), left and right medial central (LMCe and RMCe), left and right mediolateral central (LDCe and RDCe), midline parietal (MiPa), left and right mediolateral parietal (LDPa and RDPa), left and right lateral temporal (LLTe and RLTe), midline occipital (MiOc), left and right medial occipital (LMOc and RMOc), and left and right lateral occipital (LLOc and RLOc). Scalp electrodes were referenced on-line to the left mastoid; the right mastoid (referenced to the left) was also collected. Blinks and eye movements were monitored via electrodes placed on the outer canthus (the left electrode serving as reference) of each eye and the right infraorbital ridge (referenced to the left mastoid). Electrode impedances were kept below 5 k Ω . The EEG was processed through amplifiers set at a bandpass of 0.016-100 Hz, continuously digitized at 250 Hz, and stored on hard disk for later analysis.

Data analysis

Data were re-referenced off-line to the algebraic mean of the left and right mastoids (by taking the signal from each channel and subtracting half of the signal from the right mastoid). Trials contaminated by eye movements, blinks, excessive muscle activity or amplifier blocking were rejected off-line before averaging; fewer than 10% of trials were lost due to such artefacts. ERPs were computed for epochs extending from 100 ms before stimulus onset to 920 ms after stimulus onset. Averages of artefact-free ERP trials were calculated for each type of target word (ambiguous word, unambiguous noun, unambiguous verb and pseudoword) in each type of context (noun-predicting and verb-predicting) after subtraction of the 100 ms prestimulus baseline.

Results

Behaviour

On average, volunteers responded correctly 89% of the time to the comprehension probe questions (range 75–95%). Participants were somewhat more accurate (average 92%) at detecting an accurate restatement of the previous experimental sentence than at rejecting an inaccurate restatement (average 85%). Overall, the behavioural results indicate that, during the recording session, volunteers were attending to the experimental stimuli and processing them for meaning.

ERPs

Ambiguity

Figure 2 shows the grand average ERP response to all word class-ambiguous items (collapsed across their use in noun and verb contexts) overlapped with the response to unambiguous nouns and verbs (collapsed across their use in word class-appropriate contexts). Relative to the response to unambiguous items, the response to word class-ambiguous items is characterized by slow, frontal negativity, beginning

 \sim 200 ms after target word presentation and continuing into the next word in the sentence.

An omnibus analysis of variance (ANOVA) on two repeated measures [two levels of ambiguity (ambiguous versus unambiguous) and 11 levels of electrode (electrode sites used for this and subsequent analyses over the back of the head were MiCe, LDCe, LMCe, RDCe, RMCe, MiPa, LDPa, RDPa, LLTe, RLTe, MiOc, LLOc, LMOc, RLOc and RMOc] revealed a significant effect of ambiguity on the response over frontal electrode sites beginning with the P2 time window (150-250 ms) [F(1,21) = 4.25; P = 0.05] and continuing from 250 to 500 ms [F(1,21) = 6.47; P = 0.02]and into the next word (500–900 ms) [F(1,21) = 10.55;P < 0.01]. During all three time periods, word classambiguous items were more negative than their unambiguous counterparts over prefrontal and frontal electrode sites. This was the case despite the fact that the words were embedded in contexts that always rendered their word class usage unambiguous.

Word class (noun versus verb)

The left half of Fig. 3 shows the grand average ERP response to word class-ambiguous items used as nouns compared with the response to the same lexical items used as verbs; the right half of Fig. 3 shows the response to unambiguous nouns (in appropriate, noun-predicting contexts) compared with the response to unambiguous verbs (in appropriate, verbpredicting contexts).

Based on previous findings, analyses were conducted in the 250–450 ms time window over central/posterior electrode sites in order to examine the effects of word class on the N400 and in the 200–400 ms window over frontal electrode sites to examine word class effects on the P200 (Preissl *et al.*, 1995).

Central/posterior sites (N400). An omnibus ANOVA on two levels of ambiguity (ambiguous versus unambiguous), two levels of word class (noun versus verb) and 15 levels of electrode (electrode sites used for this and subsequent analyses over the back of the head were MiCe, LDCe, LMCe, RDCe, RMCe, MiPa, LDPa, RDPa, LLTe, RLTe, MiOc, LLOc, LMOc, RLOc and RMOc) revealed a significant main effect of word class [F(1,21) = 4.11; P = 0.05] on the response between 250 and 450 ms. This effect interacted with electrode [F(14,294) = 2.92; P = 0.02]. Regardless of the level of ambiguity, items appropriately used as nouns generated more negativity between 250 and 450 ms (N400) than did items appropriately used as verbs. As seen in Fig. 3, this word class difference was more prominent over medial, central sites, a distribution that is typical of N400 effects (Kutas and Van Petten, 1994).

Frontal sites (P200). An omnibus ANOVA on two levels of ambiguity (ambiguous versus unambiguous), two levels of word class (noun versus verb) and 11 levels of electrode



Fig. 2 ERP response to word class-ambiguous (both contexts) (dotted lines) and unambiguous (appropriate contexts) (solid lines) items at all electrodes. The electrode site locations are laid out as in Fig. 1. Negative is upwards in this and all subsequent figures. Over frontal electrode sites, the response to word class-ambiguous items (averaged across contexts) is more negative from ~150 ms than is the response to unambiguous items (in word class-appropriate contexts).

revealed significant main effects of both ambiguity [F(1,21) = 7.35; P = 0.01] and word class [F(1,21) = 10.23; P < 0.01] on the response between 200 and 400 ms, as well as a significant ambiguity × word class × electrode interaction [F(10,210) = 2.58; P = 0.04]. In general, ambiguous items were more negative than unambiguous items over frontal sites, as already described. In addition, items appropriately used as nouns were more negative than those used as verbs. However, as can be seen both in Fig. 3 and in the voltage maps (Fig. 4), the topographical pattern of word class differences for ambiguous and unambiguous items used as nouns were more negative than the same items used as nouns were more negative

were consistent with it being continuous with the difference observed over central/posterior sites. In contrast, the word class difference for unambiguous items was significantly skewed towards left, lateral frontal sites. Moreover, the distribution of this effect makes it unlikely to be related to the word class effects on the N400 observed over central/ posterior sites; instead, it appears that, in addition to the broadly distributed increased negativity observed for nouns, unambiguous verbs (but not ambiguous items used as verbs) elicit a left-lateralized, frontal positivity between 200 and 400 ms after stimulus onset.

Summary. Word class significantly affects the ERP response over both frontal and central/posterior sites, though the nature of this effect seems to differ between ambiguous





Fig. 3 Word-class effect for ambiguous (left) and unambiguous (right) items at eight representative electrode sites. The position of each of the electrode locations on the head is indicated by an X on the small head icon. For word class-ambiguous items, on the left-hand side, nouns (dotted lines) are more negative than verbs (solid lines) over frontal and central electrode sites between 250 and 450 ms. As shown on the right-hand side, unambiguous nouns (dotted lines) are also more negative than unambiguous verbs (solid lines) in this time window over central sites. In addition, unambiguous verbs elicit a left-lateralized frontal positivity beginning at ~200 ms; this effect is not seen for unambiguous nouns or ambiguous items in either context.

and unambiguous items. First, the exact same word classambiguous items generate more frontocentral negativity between 250 and 450 ms when they are used as nouns than when they are used as verbs. Unambiguous nouns are also more negative than unambiguous verbs between 250 and 450 ms, though this effect is confined primarily to central/ posterior sites (a distribution more canonical of the N400). In addition, relative to the response to unambiguous nouns, the response to unambiguous verbs is characterized by a left, lateral, frontal positivity; this effect is not seen in the ambiguous noun/verb comparison.

Contextual match/mismatch

The left side of Fig. 5 shows the response to unambiguous nouns used in correct (noun-predicting) and incorrect (verb-

predicting) contexts, while the right side shows the equivalent for unambiguous verbs. In general, the response to an unambiguous verb or noun in a context inappropriate for its word class is characterized by an increased negativity around 250–450 ms (N400) followed by increased positivity beginning around 600 ms (P600). Analyses were conducted in the 200–400 ms time window over frontal sites to examine contextual influences on the P200 and in the 250–450 ms and 600–900 ms time windows over central/posterior sites to examine contextual effects on the N400 and P600, respectively.

Central/posterior sites (N400 and P600). An omnibus ANOVA on two levels of contextual fit (match versus mismatch), two levels of word class (noun versus verb) and 15 levels of electrode revealed a significant main



Fig. 4 Isopotential voltage maps (at 350 ms) for nouns (correctly used in noun-predicting contexts versus incorrectly used), verbs (correctly used in verb-predicting contexts versus incorrectly used), word class-ambiguous items and pseudowords, in front and left-side views. The maps were derived by spherical spline interpolation. Red indicates positive voltages and blue indicates negative voltages. While all conditions show more positivity over frontal than over posterior scalp regions, this frontal positivity is largest for unambiguous verbs and is left-lateralized only in that condition (first column, middle plot). Note further that these items elicit such left-lateralized positivity only when they are actually used as verbs, i.e. when they correctly appear in verb-predicting contexts ('verbs, correct' but not 'verbs, incorrect'). The strength of the N400 effect, which is greatest for pseudowords, next greatest for nouns (especially in incorrect contexts), can also be seen over posterior scalp regions.

effect of word class [F(1,21) = 4.11; P = 0.05] and a significant contextual fit × word class × electrode interaction [F(14,294) = 3.13; P < 0.01] between 250 and 450 ms. As described previously, unambiguous nouns elicited greater negativity (N400) than unambiguous verbs, whether they matched or mismatched the context. In addition, over medial central sites, unambiguous nouns (but not unambiguous verbs) elicited greater negativity when they occurred in mismatching (i.e. verb-predicting) than matching (i.e. noun-predicting) contexts.

The same analysis conducted in the 600–900 ms time window revealed a significant main effect of contextual fit [F(1,21) = 8.44; P < 0.01] and a significant contextual fit × electrode interaction [F(14,294) = 4.48; P < 0.01]. The

responses to both unambiguous nouns and unambiguous verbs were associated with increased positivity between 600 and 900 ms after stimulus onset, when they mismatched their context relative to when they fitted. This effect was largest over central, posterior (occipital and parietal) sites, a distribution observed typically for the P600 (Coulson *et al.*, 1998).

Frontal sites (P200). An omnibus ANOVA on two levels of contextual fit (match versus mismatch), two levels of word class (noun versus verb) and 11 levels of electrode revealed a significant main effect of contextual fit [F(1,21) = 11.32; P < 0.01] and a significant contextual fit × word class × electrode interaction [F(10,210) = 2.33; P = 0.05].



Fig. 5 Context effects for unambiguous nouns (left) and verbs (right) at eight representative electrode sites. When class-unambiguous items are used inappropriately in sentence contexts (noun in a verb context or verb in a noun context) (dotted lines), the ERP response relative to their appropriate use (noun in a noun context or verb in a verb context) (solid lines) is characterized by increased negativity between 250 and 450 ms (N400), which is larger for the inappropriate use of nouns, followed by a large late positivity. The left-lateralized frontal positivity elicited by unambiguous verbs in inappropriate contexts is not apparent when these same items are used in noun-predicting contexts.

Overall, mismatch between an unambiguous item's lexical class and the lexical class demanded by the context was associated with greater negativity in this time window; this was probably the frontal continuation of the N400 effect described for central/posterior sites. The interaction arose because, as can be seen in Fig. 5 and in the voltage maps in Fig. 4, the left, frontal positivity observed for unambiguous verbs (but not unambiguous nouns) was present only when they matched the word class predicted by the context.

Noun in a noun context

Noun in a verb context

(the) beer

(to) beer

.....

Summary. Fit to context influenced the ERP response over central/posterior sites in both the N400 and P600 time window and also influenced the left, frontal positivity (P200?) observed over frontal sites. Unambiguous items used in word class-inappropriate sentence contextual frames elicited P600 responses and, in the case of unambiguous nouns, enlarged

N400s relative to the same items appearing in appropriate (matching) contexts. In addition, unambiguous verbs in mismatching contexts did not elicit the left, frontal positivity that was observed to these same lexical items used appropriately.

Verb in a verb context

Verb in a noun context

(to) eat

(the) eat

.....

Right

Stimulus type (real word versus pseudoword)

Figure 6 shows the responses to pseudowords used as nouns and pseudowords used as verbs overlapped with the response to real (word class-ambiguous) words collapsed across context. Here, we contrasted pseudowords with ambiguous real words, as they too can appropriately appear in either noun- or verb-predicting contexts. Relative to real words, pseudowords elicited increased negativity over most electrode sites between 250 and 450 ms and increased positivity over



Fig. 6 ERP response at all electrodes to pseudowords used as verbs (dotted lines) and pseudowords used as nouns (dashed lines), contrasted with the response to real (word class-ambiguous) words (solid lines). In general, pseudowords elicit larger N400 responses and larger late positivities than do real words that also can be used in either type of sentence context. In addition, the response to pseudowords used as verbs is more negative 250–450 ms after stimulus onset than the response to these items used as nouns.

central/posterior sites, beginning ~600 ms after stimulus onset.

For the 250–450 ms time window, an omnibus ANOVA on two levels of stimulus type (real word versus pseudoword), two levels of word class (noun versus verb) and 26 levels of electrode revealed a significant main effect of stimulus type [F(1,21) = 14.94; P < 0.01], a stimulus type × word class interaction [F(1,21) = 6.09; P = 0.02], and a stimulus type × electrode interaction [F(25,525) = 7.11; P < 0.01]. In both noun-predicting and verb-predicting contexts, the response to pseudowords was associated with increased negativity relative to the response to real words. As can be

seen in Fig. 6, this stimulus type difference was more pronounced over central/posterior sites and was larger over the left than over the right scalp. However, while the response to real (ambiguous) words used as nouns was more negative than the response to the same items used as verbs, for pseudowords the reverse was true: that is, pseudoword responses were more negative in verb-predicting than in noun-predicting contexts. As was true for ambiguous words used as verbs, pseudowords used as verbs did not elicit the left, frontal positivity observed for unambiguous verbs.

The same analysis conducted in the 600–900 ms time window revealed a main effect of stimulus type [F(1,21) = 5.98; P = 0.02] and a stimulus type × electrode interaction [F(25,525) = 11.64; P < 0.01]. Independently of whether the context was noun- or verb-predicting, pseudowords elicited greater positivity 600–900 ms after stimulus onset (P600) than did real words in the same contexts. This effect was most prominent over posterior electrode sites, a distribution similar to that seen for unambiguous items used in inappropriate contexts and typical of a P600 response.

General summary

The three types of stimuli used in the experiment, i.e. word class-ambiguous items, unambiguous words and pseudowords, were all associated with different ERP responses. Throughout their course, the response to word classambiguous items was more negative than the response to word class-unambiguous items. Furthermore, relative to real (ambiguous) words, pseudowords elicited increased N400 and P600 responses. Unambiguous items embedded in inappropriate (word class mismatching) contexts also elicited increased N400 and P600 responses.

Despite overall differences, effects of word class (noun versus verb) were found for all stimulus types. However, the nature of this word class effect varied with the type of stimulus. Pseudowords elicited greater N400 responses when used as verbs than when used as nouns. In contrast, ambiguous items elicited greater frontocentral negativity between ~200 and ~450 ms when they were used as nouns than when they were used as verbs. The response to unambiguous nouns was also more negative than the response to unambiguous verbs over central-parietal sites between 250 and 450 ms (N400). In addition, unambiguous verbs elicited a unique left-lateralized frontal positivity that was not observed for unambiguous nouns or for any of the other stimulus types. However, this positivity was observed only when the unambiguous verbs were embedded in appropriate contexts-in other words, when they were actually used as verbs.

Discussion

The aim of this study was to examine word class-related ERP differences systematically so as to determine whether the effects observed are a function of differences in the neural representation of nouns and verbs, differences in how these word classes are processed on-line, or differences in both of these. To this end, we compared the electrical responses of the brain to three types of stimulus: pronounceable pseudowords with no prior lexical representation, unambiguous nouns and verbs, and word class-ambiguous items that have both noun and verb senses. Each stimulus type was embedded in sentence contexts that unambiguously called for either a verbal or a noun phrase continuation at the target comparison point; the two types of sentence contexts were otherwise held as similar as possible. By examining the ERP response to the different types of targets as a function of context, we could examine the

influence of stimulus type, word class and the interaction of the two on neural processing.

Stimulus type had clear main effects on the ERP waveform. Pronounceable pseudowords elicited increased central negativity from 250 to 450 ms and increased posterior positivity from 600 to 900 after stimulus onset relative to real words and, in particular, relative to word class-ambiguous items that, like the pseudowords, fitted both noun- and verbpredicting contexts equally well. The finding of greater N400 activity in response to pseudowords has been reported previously (e.g. Bentin et al., 1985; Ziegler et al., 1997) and may be taken to reflect the system's attempt-and failureto find associated lexical-semantic information for these pronounceable letter strings in long-term memory. In addition, in this experiment pseudowords also elicited an increased late positivity (P600) that was similar in time course and distribution to that observed when unambiguous words were used in inappropriate contexts; this component has been linked to difficult/improbable syntactic processing (e.g. Osterhout and Holcomb, 1992; Coulson et al., 1998). Here, pseudowords were embedded in the middle of sentences, encouraging participants to attempt to assign syntactic properties (such as word class) to the novel items in order to build a sentence representation that would allow them to parse upcoming words accurately. The P600 in response to the pseudowords indicates that making such assignments for novel items is difficult, but not contingent on the prior existence of a lexical representation in the mental lexicon. In general, therefore, the ERPs in response to novel, pronounceable strings of letters reflect the brain's attempt to deal with the problem of incorporating unknown lexical items into an ongoing sentence context.

We also observed ERP differences between the two types of real words: those that were ambiguous with respect to word class and those that were not. This difference is particularly striking because in our study target words always appeared in disambiguating sentence contexts. That is, while target items were labelled as 'ambiguous' when they could be used as both legal English verbs and legal English nouns, the semantic and syntactic referents (and hence word class) of these items were never ambiguous in the sentence contexts themselves (e.g. 'He prepared to paint . . .'). Note that these ambiguous items are in no way peculiar or obvious; indeed, a large proportion of the most common and familiar words in the English language are word class-ambiguous. Furthermore, participants saw each ambiguous item only once, used either as a noun or a verb, and during debriefing almost all reported being unaware of the fact that some of the items used in the study could have appeared felicitously in the opposite type of context while others could not. The distinction between the two stimulus types, however, is clearly important to the brain: relative to unambiguous words, ambiguous items were associated with a slow, frontal negativity beginning at ~150 ms and continuing into the next word. This was true despite the fact that these items appeared in the same contexts and were matched for both word length and word frequency.

Prior studies reporting the effects of ambiguity on ERPs have focused primarily on situations wherein the ambiguity is present in the experimental context itself. Osterhout and colleagues, for example, observed a P600 response at the point of disambiguation in syntactically ambiguous sentences in which participants experienced a 'garden path' effect (e.g. at 'was' in 'The lawyer charged the defendant was lying'). (Osterhout and Holcomb, 1992; Osterhout et al., 1994). In a similar paradigm, Hopf and colleagues observed an increased N400 in response to a disambiguating verb following a caseambiguous noun phrase; they observed no ERP difference, however, in response to the ambiguous noun phrase itself when compared with unambiguous controls (Hopf et al., 1998). Only one prior study has examined the response to lexically/semantically ambiguous words in a disambiguating context: Van Petten and Kutas used homographs, half of which were word class-ambiguous and thus similar to those used in this study (e.g. 'The logger cut down the tree with a chain saw'). They found no ERP differences when these ambiguous items were compared with unambiguous controls, suggesting that, at least with moderately strong semantic contexts, only the contextually relevant meaning of an ambiguous word is accessed (Van Petten and Kutas, 1987). Note that the present study differs from that of Van Petten and Kutas in that our method provided the disambiguation via syntactic (i.e. prior presentation of 'to' versus 'the') as opposed to semantic cues. Under these circumstances, the processing of ambiguous items does seem to involve additional/different neural resources compared with the processing of unambiguous items.

The brain thus responds differently to pseudowords as opposed to real words and to word class-ambiguous as opposed to unambiguous items. Does the brain also respond differently to nouns and verbs, or items used as nouns and verbs? If so, is this effect similar across the different types of stimuli? We found that word class affected the ERP response for all stimulus types. Importantly, however, the nature of this effect differed across all three stimulus types. Pronounceable pseudowords elicited greater N400s when they were used as verbs than when they were used as nouns. It seems, therefore, that semantic processing of a novel item is more taxing when that item is in a verbal sentence position than when it is used as a noun. This may reflect the fact that English more readily permits the coinage of new nouns than of new verbs; the effect may also arise because the semantics of verbs is more complicated than that of nouns (e.g. Langacker, 1987) and correspondingly more difficult to 'guess' from contextual information when an unfamiliar lexical item is encountered. The word class effect observed for pseudowords, however, was not observed for either type of real word. Thus, we did not find evidence to suggest that there is a general set of neural resources that is differentially recruited whenever a potentially meaningful lexical item is processed as a noun versus as a verb.

Like pseudowords, word class-ambiguous items are grammatical in either noun- or verb-predicting contexts. Still,

the word class difference we observed in the response to ambiguous items went in the opposite direction from that observed in the response to pseudowords. In this case, it was word class-ambiguous items used as nouns that elicited increased negativity over both frontal and posterior sites relative to the response to the same lexical items used as verbs. A similar effect was observed for unambiguous nouns relative to unambiguous verbs, though the difference was smaller and confined to more posterior electrode sites. Brown and colleagues also observed increased negativity over posterior sites in response to word class-ambiguous items used as nouns rather than as verbs (Brown et al., 1973, 1976, 1980); however, this effect reversed over frontal sites in their studies, whereas we found greater negativity for ambiguous items used as nouns over all electrode sites. There are several reasons why the topography of the observed effect might have differed between these studies, including the fact that the experiments of Brown and colleagues were conducted in the auditory modality and employed massive repetition (participants listened to alternating blocks of 30 repetitions of the same phrase). However, when we focus on the response over posterior electrode sites, across these studies there is the suggestion that the N400 response to nouns-and to ambiguous words used as nouns-may be larger than the N400 response to verbs and ambiguous items used as verbs. [Brown and colleagues observed the opposite effect: increased N400 activity to verbs relative to nouns in Dutch (Brown et al., 1999). However, their nouns and verbs were not matched for word frequency or length, so it is difficult to tell what factors may have contributed to the effect in that study.] In addition, in our study we found evidence for a bilateral frontal effect (or a much more frontally distributed N400 effect) that distinguishes noun processing from verb processing when ambiguous items are used in word classpredictive contexts.

Whereas the word class effect for unambiguous and ambiguous items was similar over posterior sites, a qualitatively different effect was observed over frontal sites. Unambiguous verbs properly used as such elicited a left, lateral positivity over prefrontal and frontal electrode sites relative to appropriately used unambiguous nouns. This lateralized positivity was unique to unambiguous verbs; we did not observe it to nouns in any condition or in response to pseudowords or ambiguous real words used as verbs (despite the fact that the latter class of items contains many very common English verbs). This brain potential thus seems to index something about a word's lexical status as an unambiguous verb. It appears to be similar to the left, frontal positivity observed in response to action verbs in the study by Dehaene (Dehaene, 1995) (although one-third of their verbal items were actually word class-ambiguous). It may also be related to the P200 response reported by Preissl and colleagues (Preissl et al., 1995) (who conducted their study in German, a language in which word-class ambiguity is rare), though their response was more focal in time; the comparison is difficult to make definitively, as Preissl and

colleagues show waveforms for only one central and one occipital site (Preissl *et al.*, 1995), whereas the positivity observed here and reported by Dehaene was largest over lateral, frontal sites (Dehaene, 1995). Pulvermüller and colleagues have suggested that the P200 response specifically reflects something about a word's semantic associations with motor activity (Pulvermüller, 1999; Pulvermüller *et al.*, 1999b). However, if the response we observe is indeed related to the P200, it is notable that we observed it in response to a broader class of items than action verbs. More importantly, it is noteworthy that we did not observe this response to ambiguous items used as verbs, despite the fact that the ambiguous set of verbs contained roughly as many items with motor associations as did the unambiguous set.

While the left, frontal positivity we observed in response to unambiguous verbs seems to index something about these items' lexical status, the effect is nevertheless sensitive to context. When the same unambiguous verbs are encountered in inappropriate contexts, i.e. when the context sets up an expectation of a noun, the positivity is not observed. Thus, this ERP effect clearly does not derive from some inevitable semantic or lexical property of these unambiguous verbs. Instead, the brain response seems to reflect an interaction of representational and processing factors: it is observed to only some legal English verbs (those that are unambiguous) and only when they are appropriately playing their verb role in a sentence context (and, perhaps, also when these items are seen in isolation). One might speculate, therefore, that this response reflects something about the particular semantic or syntactic roles of verbs in language, roles that are suppressed when these items are placed in a noun position in context. Word class-ambiguous items, of course, also play these roles when used as verbs, yet they do not elicit a left frontal positivity. This suggests that the representation of ambiguous and unambiguous items is fundamentally different, such that even when they are used unambiguously in context they engage different neural resources for processing. We thus do not see the response one would predict if the representation of these ambiguous items were made up of two separate lexical entries similar in all other respects to those of unambiguous items.

Unambiguous verbs in noun-predicting contexts, like unambiguous nouns in verb-predicting contexts, elicit an increased N400 followed by a P600. As was true for pseudowords, therefore, the processing of unambiguous items in word class-inappropriate contexts renders both semantic and syntactic analyses more difficult. The inappropriate use of a noun in a verb context elicited a larger N400 effect than did the inappropriate use of a verb. This is also similar to the effect seen with pseudowords, which elicited larger N400 responses in verb than in noun contexts. Again, therefore, it seems to be more difficult to semantically 'fill in' for inappropriate or missing verb information than to do so for inappropriate or missing noun information. The inappropriate use of unambiguous items also elicited a P600—of equal size for both nouns and verbs—most likely reflecting the improbability and difficulty of the syntactic construction created in these cases.

In summary, we set out to see if we could find evidence, in the intact adult brain, for the differential representation of nouns and verbs. To do this, we examined word class differences in context, so that the contributions of representation and processing could be assessed. We also designed our study to allow us to examine the neural representation of word class-ambiguous items. We did, in fact, find word class-related ERP differences for all the types of stimuli we compared-pseudowords, unambiguous items and word class-ambiguous items-albeit different in nature for each type. While word class seems to be a variable that has definite effects on neural representation and processing, therefore not surprisingly from a neurobiological perspective these effects are modulated by the nature of the stimulus as well as the context in which that stimulus appears. Although our findings are at a more complex level of representation, they are thus similar to those emerging from detailed studies of representation and processing within sensory areas, such as the visual system. Items with different features tend to activate different sets of cells (for single-cell recording studies in the inferotemporal cortex, see e.g. Tanaka, 1996), but the precise mapping of the features and the extent to which a given cell actually becomes active in response to a stimulus is a function of both the contexts in which the stimulus has tended to appear in the past and the nature of the current context (e.g. Sakai and Miyashita, 1991, also in the inferotemporal cortex).

Some of the differences we observed are probably related specifically to how nouns and verbs are processed in context. For example, we found that the semantic processing, as indexed by the N400 response, of both pseudowords and incorrectly used unambiguous lexical items was more difficult when these items were in a verb position in a sentence than when they were in a noun position. Interruption of processing at the position of the verb thus seems to be more taxing for the system, perhaps because the semantic information conveyed by verbs, being relational in nature, is more critical for the maintenance of discourse coherence (Langacker, 1987). We also observed that the response to nouns and ambiguous items used as nouns was more negative posteriorly ~250 ms after stimulus onset than was the response to verbs or ambiguous items used as verbs. It is possible that the semantic information conveyed by verbs, when correct, is somewhat more predictable, and therefore easier to integrate, than is the semantic information conveyed by nouns. This seems consistent with the observation of Gentner that noun information is less likely to be altered in paraphrase or translation (Gentner, 1981), possibly because this information is more specific and thus less predictable.

Some word class effects, therefore, seem to be related to the roles that lexical items are playing in a sentence or larger unit of discourse, serving as pointers to specific information, for example, or providing a relational structure for that information. However, we also found word class effects that

suggested lexically based neural representational differences as well. In particular, we observed a left anterior positivity, similar to that seen in several previous studies in response to isolated action verbs (Dehaene, 1995; Preissl et al., 1995), that was specific to those lexical items that were unambiguous English verbs. It distinguished these unambiguous verbs not only from unambiguous nouns but also from word classambiguous items that, in at least one of their senses, could be used as a legal English verb. These results support the notion that different neural networks support the representation of nouns and verbs. However, the results also make it clear that word class-ambiguous items, in languages like English, constitute yet another class of lexical items with a distinct neural representation. The ERP response to these ambiguous items, even in disambiguating contexts, was different from the response to either type of unambiguous item. The results thus suggest that different neural resources are used not only for the representation of verbs as opposed to nouns but also for the representation of items that can appear in multiple syntactic and semantic roles, even though these ambiguous items have typically not been afforded separate status in many theories about word class representation and processing (e.g. Damasio and Tranel, 1993; Pulvermüller, 1999). From a neuropsychological standpoint, this means that the dissociations between nouns and verbs that have already been described (e.g. Damasio and Tranel, 1993; Daniele et al., 1994) are likely to be modulated by ambiguity. The findings also imply the likelihood of further lexical processing dissociations between word class-ambiguous and unambiguous items which, if observed, would provide additional information about the neural organization of lexical representation.

Finally while we found evidence for neural representational differences based on word class, we also found clear support for on-line interactions between representation and processing. Specifically, we observed that the left frontal positivity elicited by unambiguous verbs in appropriate contexts was suppressed when these same lexical items appeared incorrectly in a noun position in the sentence. It seems, therefore, that from an early point in a word's processing, context acts to direct the search for word classrelated information, such that, even if a lexical item is unambiguously a verb, it is not processed as such when it appears in the wrong syntactic role in context. Word class, therefore, does not appear to be an inherent, immutable property of lexical items or of particular positions in the sentence structure. An unambiguous verb is processed differently depending on the syntactic role it is playing in context; an item in the verb position of a sentence is processed differently if it is unambiguously a verb as opposed to if it can sometimes appear as a noun. Whether one is likely to observe a word class-based dissociation in a neuropsychological population and the type of dissociation observed will, therefore, depend critically not only on the items that are tested but also on the context in which those items appear and on the nature of the task to be performed.

Thus, while the results from this experiment suggest that the brain does indeed represent, and process, different types of lexical items in different ways, the results also show that word class does not 'reside' in a neural representation, but rather emerges—in real time—from an interaction of semantic and syntactic properties at both the single-word and the discourse level.

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