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Electrophysiological evidence for category-specific word processing in the normal human brain

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SELECTIVE impairment of word categories such as nouns *vs* verbs has suggested a regional representation of lexical knowledge in the human brain. The time course of visual word processing was investigated using event-related potentials (ERPs) in normal adults. Subjects performed a word classification task with five categories of stimuli: animal names, verbs, numerals, proper names and meaningless consonant strings. A bilateral posterior ERP difference between words and consonants first appeared 192 ms following stimulus onset, probably reflecting the construction of the visual word form. Category-specific ERP differences began to appear around 260 ms. There was a left temporo-parietal negativity for animal names and verbs, a left inferior temporal negativity for proper names, and a bilateral positivity for numerals. These results provide [redacted] evidence for timing and coarse localization of category-specific word processing in the normal human brain.

Key words: Event-related potentials; Human brain mapping; W d recognition; Lexical access; Temporal lobe; Hemispheric asymmetry; Proper names; Numerals

Introduction

Various neurological conditions, including left perisylvian stroke, herpes simplex encephalitis and progressive degenerative disease, may cause highly specific impairments of word processing, with a drastic loss of certain categories of knowledge.[1–5] For instance, a patient may be completely unable to define names of foods and animals, while providing precise definitions for names of man-made objects.[2] Likewise, in word production, a double dissociation is found between verb retrieval and noun retrieval.[3,4] Category-specific dissociations have been reported for categories as different as abstract *vs* concrete words, living things *vs* inanimate objects, verbs *vs* nouns, animals, fruits and vegetables, body parts, colour names, proper names, numerals, etc, suggesting a remarkably specific regional organization of lexical and semantic knowledge in the human brain. Classical neuropsychological models of lexical access in the visual modality distinguish three stages in visual word processing: visual analysis of stimulus shapes, construction of a structural representation of the letter string (visual word form), and access to lexical and semantic information.[1,5] The present experiment was designed to measure the timing and coarse brain localization of these stages in normal subjects, and to study if, when and where category-specific responses would be found. Event-related potentials (ERPs) were recorded from 64 scalp electrodes while normal adults performed a classification task with visually presented words. The words could be animal names, action verbs, proper names of famous persons, or numerals. Consonant strings were also used as a control.

Based on the above model, the following predictions were made. First, early visual analysis, as indexed by the early components of the visual ERP, should not differ across the five categories because the stimuli were matched for length, size, and font. Second, the visual word form should be constructed only for words but not for consonant strings. Hence it was predicted that all words would simultaneously diverge from consonant strings, and that the onset and scalp localization of this divergence would reflect the time of activation and coarse brain localization of the visual word form system. Third, later in time, inasmuch as different word categories activate partially different brain regions, the ERPs evoked by the four categories of words should also diverge. Again, the onset and scalp localization of the differences should give clues as to the time of activation and coarse brain localization of category-specific knowledge in the normal human brain.

Materials and Methods

Thirty stimuli, 3–9 letters long, were selected within each of five categories: animal names, action verbs, names of famous persons, numerals, and consonant strings. The stimuli were organized in quintuplets matched for length (example: chicken, whisper, clinton, fifteen, cpvlrfn). As far as possible, the words were matched for number of syllables and letter content. Numerals and verbs were also matched for frequency of occurrence.[6] By necessity, the frequency of animal names and of proper names was one order of magnitude smaller. However all words were rated as highly familiar by four native speakers of American. By contrast, all consonant strings, created by randomly combining the same consonants used in the words, were judged as meaningless. Ambiguous words such as duck (verb or animal) were systematically avoided. One-third of the verbs could also be common nouns (e.g. walk, laugh), but the frequency as a noun was considerably lower than the frequency as a verb.

The stimuli were written in capital letters and were flashed for 150 ms, white on black, onto a computer screen, in eight short lists of 67–68 words. Subjects had to monitor each list for words of a given category (e.g. animals) and to make a bimanual yes–no response to each word. The side of the 'yes' response was randomized within subjects. Each list comprised all 30 words from the target category, 10 words from each of the three other non-target word categories, and seven or eight consonant strings. Thus, at the end of experiment, each subject had responsed four times to each word (twice as a target, twice as a non-target) and twice to each consonant string (always as a non-target).

Twelve right-handed male University of Oregon students (mean age 20.9 years) volunteered to serve as subjects. All gave written informed consent, and the procedure was approved by the human subjects ethical committee of the University of Oregon. ERPs were collected using a 64-channel geodesic electrode net[7] referenced to the right mastoid, and digitized at 250 Hz over a 1 s epoch including a 150 ms prestimulus baseline. Erroneous trials, or trials with electrical or eye movement artifacts, were automatically rejected (21.2% of trials). The remaining trials were averaged and transformed into reference-independent values using the average-reference method.[7] Three-dimensional reconstructions of scalp voltages at each time step were computed using spherical spline interpolation and back-projection on a realistic head model.

Four time windows were selected for statistical analysis: 64–108 ms (peak of the posterior P1), 120–156 ms (peak of the posterior N1), 200–276 ms (peak of the posterior P2), and 280–356 ms (peak of left temporal N2). For each window, the average voltage was computed for selected channel pairs and for each stimulus category, and submitted to a 5 (stimulus category) × 2 (hemisphere) repeated-measures analysis of variance (ANOVA). When the main effect of category was significant, planned comparisons were used to assess global differences between words and consonant strings, as well as differences among the four categories of words. When a significant effect was found ($p < 0.01$), its onset time was determined using sample-by-sample F-tests, with a criterion of $p < 0.01$ for five successive samples.

Results

The average RT was 510 ms and the overall error rate was 3.2%. An ANOVA uncovered small but consistent differences in RT and error rates across the five categories of stimuli (respectively $F(4,44) = 20.63$, $p < 0.0001$; $F(4,44) = 6.02$, $p = 0.0006$). A planned contrast indicated that consonant strings were classified faster (493 ms) and more accurately (1.1% errors) than words ($p = 0.007$). Among the words, numerals were classified faster than other categories ($p = 0.0004$; numerals, 484 ms; animal names, 513 ms; proper names, 524 ms; verbs, 537 ms).

Subjects were significantly faster for target than for non-target responses ($F(1,11) = 17.9$, $p = 0.0014$). ERPs also showed a large difference between target and non-target trials in the latency and amplitude of a midline fronto-central positivity which peaked at the time of the key press. This effect was late, however (onset > 250 ms), and was weak over the posterior parieto-temporal sites on which the most salient word difference were found. For present purposes, therefore, target and non-target trials were pooled and ERPs were analysed only as a function of stimulus category. Very similar results, not reported here, were obtained when only non-targets trials were analysed.

The time course and topography of ERPs to the different categories of stimuli are shown in Figures 1 and 2. No significant difference between conditions was found on the P1 and N1 time windows. The only significant effect was a consistent hemispheric asymmetry, the N1 being much larger on the left than on the right for all categories of stimuli ($p = 0.0013$). The first significant difference between the five categories of stimuli was found on the time window spanning 200–276 ms after stimulus onset, ($p = 0.0015$). There was a difference between words and consonant strings ($p = 0.0057$), but no significant difference among the four categories of words ($p < 0.07$). ERPs to each word category were significantly more positive than ERPs to consonant strings over bilateral parieto-occipital electrodes. This effect first reached significance 192 ms after stimulus onset, and reached a maximum at 248 ms.

On a window spanning 280–356 ms after stimulus onset, significant differences emerged between the four categories of words ($p < 0.0001$). At this time, ERPs were dominated by a temporo-parietal negativ-

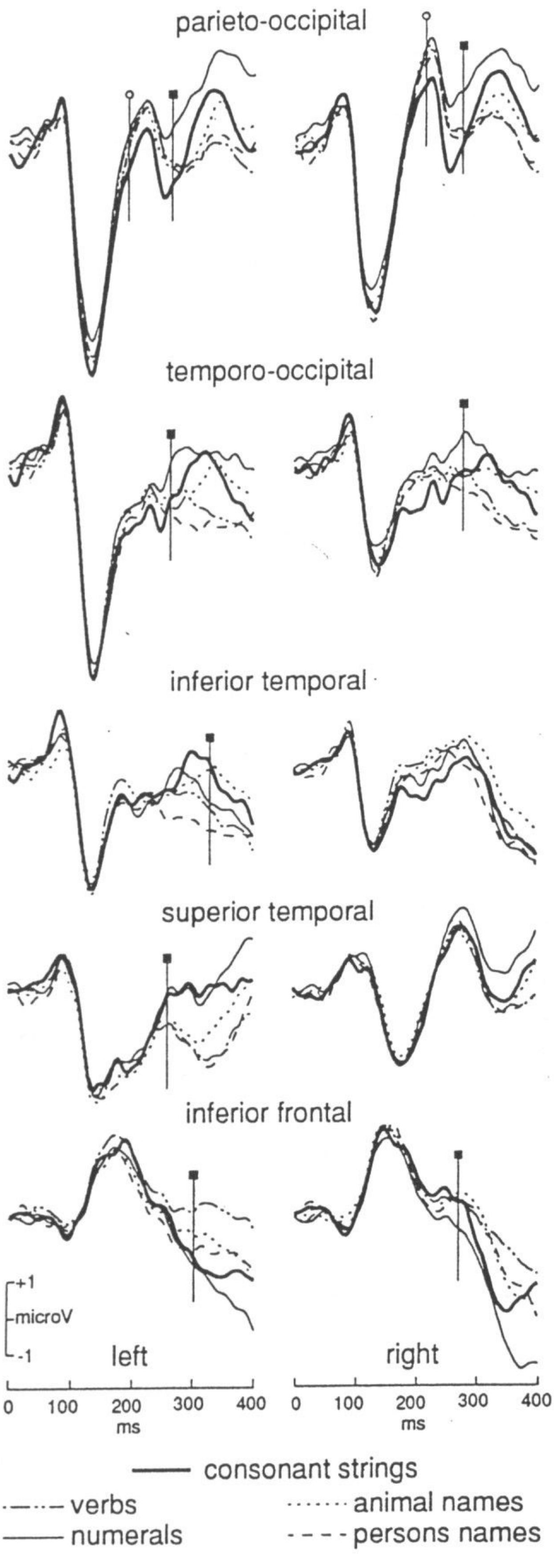

FIG. 1. ERPs evoked by the five categories of stimuli over a 400 ms epoch starting at stimulus onset. Salient left and right electrode sites were selected for illustration. Note the unaffected bilateral P1 and left-lateralized N1 on temporo-occipital sites. ○, the first significant divergence between words and consonant strings; ■, the first significant divergence between the four categories of words.

ity sharply lateralized to the left hemisphere (Fig. 2). The exact topography, however, varied with word category. For proper names, the left temporal negativity extended downwards towards left inferior temporal sites, with a similar tendency on the right. For verbs and animal names, essentially identical left temporal negativities were noted, but there was an additional left inferior frontal positivity specific for verbs. Finally for numerals, the left temporal negativity was greatly reduced. Instead, numerals elicited a bilateral parietal positivity relative to consonant strings. These category-specific differences first became significant 256–280 ms after stimulus onset, depending on electrode site.

Discussion

Several word prcessing stages were identified. An early visual ERP component, the P1 (84 ms), showed no difference between conditions and no hemispherical asymmetry, hence possibly indexing early visual processing. A second ERP component, the N1 (138 ms), again showed no difference between conditions, but was significantly left-lateralized. In previous experiments, a left-lateralized N1 was observed with words,[8–11] but a bilateral N1 was found with digit stimuli.[9] Hence, the left-lateralized N1 may index visual recognition processes specific for letter strings such as the earliest stages of visual word form construction.[12] Neuropsychological and functional imaging data indeed point to an involvement of the left ventro-mesial occipito-temporal pathway in the visual word form.[5,13]

In the present study, the left lateralized N1 was observed for words and for consonant strings, suggesting that visual word form construction was initially attempted even for consonant strings. By 200–250 ms, however, words had clearly diverged from consonant strings on bilateral parieto-occipital electrodes. This observation, which replicates previous results,[8] suggests that visual word form construction was still in progress for words, whereas it had been interrupted for consonant strings because they lacked recognizable graphemes.[13]

By 250–280 ms after the stimulus, category-specific differences appeared in ERPs. Note that the visual appearance of the stimuli provided no indication about the category to which they belonged. Hence, the fact that category membership affected ERPs implies that at this point, lexical and/or semantic

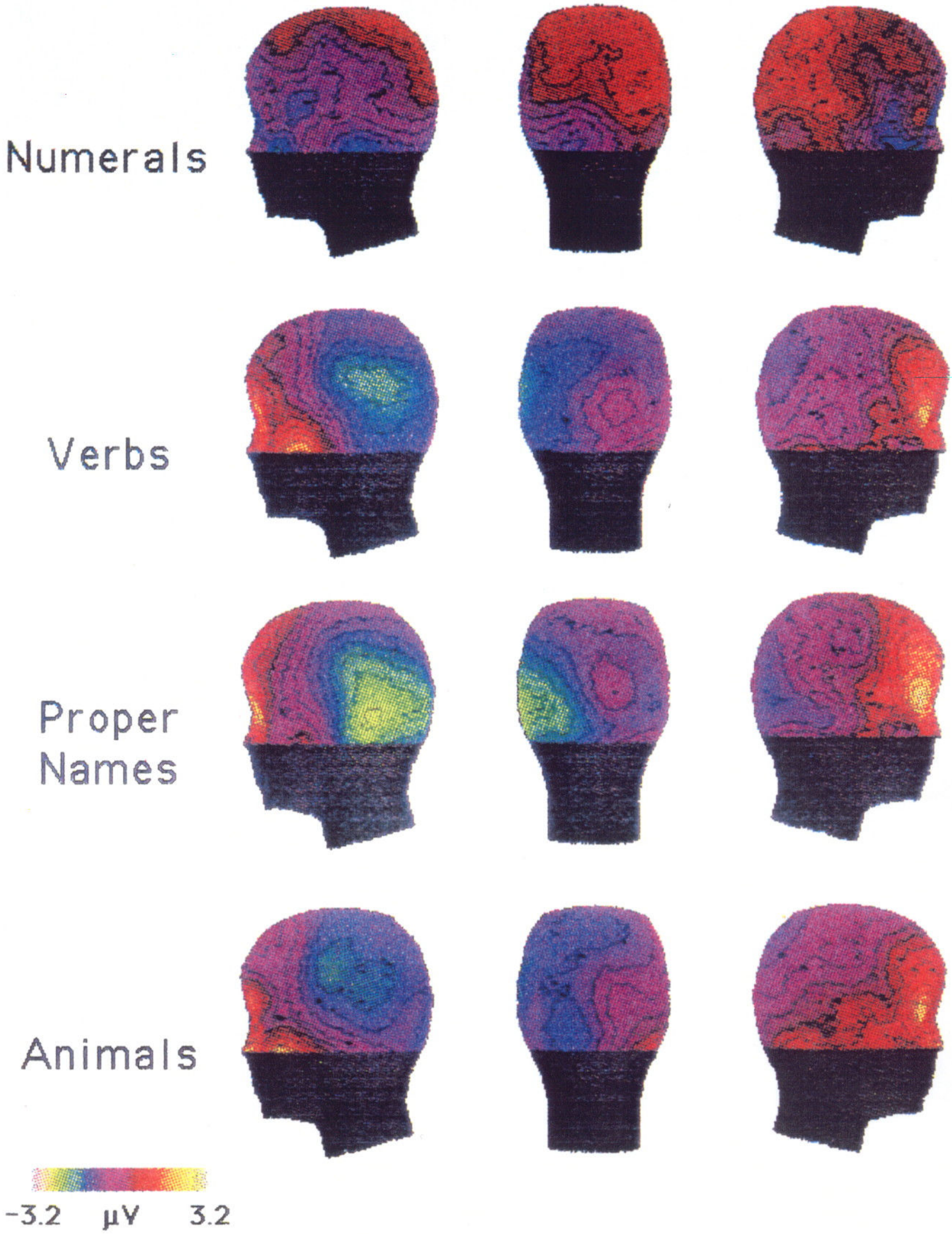

FIG. 2. Topography of the grand-averaged subtraction of ERPs to specific categories of words minus ERPs to consonant strings. Left, back, and right views of the head are shown at the peak of the left temporal negative (304 ms after stimulus onset). Voltages are colour-coded using the scale shown at bottom left.

knowledge about the words had been accessed. Furthermore, it suggests that such knowledge is represented in partially separate brain regions for different categories of words. Inferences about localization must be drawn with great care because the topography of ERPs was obviously more complex than could be produced by a single dipole (Fig. 2). Nevertheless, the strongly lateralized left temporal negativity suggests that most categories of words draw heavily on the left temporo-parietal region. This is in agreement with classical neuropsychological and brain imaging findings which attribute to this region a crucial role in the lexical and semantic representation of single words.[1,14,15]

Remarkably, numerals were the only category not to yield a left temporal negativity, but a bilateral parietal positivity. In an ERP study of number comparisons with arabic digits or written numerals, a bilateral parietal effect was also found on the very same electrode sites.[9] The involvement of the left, and to a lesser extent the right inferior parietal areas in number processing is well-known from both neuropsychological[1] and brain-imaging studies.[16,17] ERPs suggest that this specific region, rather than an all-purpose left temporal semantic network, is active during the semantic classification of numerals.

There were also suggestions of brain activations specific to the other word categories. The inferior extension of the left temporal negativity, observed only when proper names were presented, may be related to the known involvement of left and right inferior temporo-occipital areas in face processing.[1,18] Indeed, left temporal lesions may yield a specific deficit in accessing and retrieving proper names, which may be restricted to persons names.[19] With verbs, a small but specific left inferior frontal positivity was seen. Damasio and his colleages found that two patients with a left inferior frontal lesion suffered from a selective impairment in verb retrieval, with selective preservation of noun retrieval, whereas the converse dissociation was observed in case of a left temporal lesion.[4] Our results seem compatible with a putative left inferior frontal specialization for the representation of complex actions denoted by verbs,[4] although there was surprisingly little difference in the electrical activity evoked by animal names and by verbs. Animal names yielded mostly a widespread left temporo-parietal negativity, in line with reports of selective impairments of the category of 'living things' in diffuse left temporal pathologies.[1,2]

Conclusion

The present study represents a first attempt at localizing and timing lexical access for different categories of words. Category-specific knowledge about words begins to be retrieved after about 250–280 ms. While the left temporal lobe is globally involved, additional parietal, inferior temporal and inferior frontal areas may also contribute to knowledge retrieval within specific lexical or semantic categories of words. Given the spatial inaccuracy inherent to ERP research, these results await replication and extension using positron emission tomography or functional magnetic resonance imaging.

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