Perceptual and semantic sources of category-specific effects: Event-related potentials during picture and word categorization

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In two experiments the effect of object category on event-related potentials (ERPs) was assessed while subjects performed superordinate categorizations with pictures and words referring to objects from natural (e.g., animal) and artifactual (e.g., tool) categories. First, a category probe was shown that was presented as name in Experiment 1 and as picture in Experiment 2. Thereafter, the target stimulus was displayed. In both experiments, analyses of the ERPs to the targets revealed effects of category at about 160 msec after target onset in the pictorial modality, which can be attributed to category-specific differences in perceptual processing. Later, between about 300–500 msec, natural and artifactual categories elicited similar ERP effects across target and category modalities. These findings suggest that perceptual as well as semantic sources contribute to category-specific effects. They support the view that semantic knowledge associated with different categories is represented in multiple subsystems that are similarly accessed by pictures and words.

The present study was aimed at clarifying the role of perceptual and semantic processes contributing to category-specific effects by measuring event-related brain potentials (ERPs) during an object categorization task. Studies on category-specific effects in semantic memory tasks have become increasingly important to uncovering the structure of the semantic system. This field of semantic memory research originated in neuropsychological studies with brain-damaged patients, who occasionally exhibit a selective loss of semantic knowledge in some categories. A large number of brain-damaged patients have meanwhile been reported to have selectively lost their semantic knowledge about natural (or animate/living) categories (e.g., animals, vegetables) while still showing preserved knowledge about objects from artifactual (or inanimate/nonliving) categories (e.g., tools, musical instruments; De Renzi & Lucchelli, 1994; Warrington & Shallice, 1984). The opposite pattern has also been observed, albeit less frequently (e.g., Sacchett & Humphreys, 1992; Warrington & McCarthy, 1987).

Likewise, neuroimaging studies in healthy volunteers have revealed category-specific brain activation during picture naming (e.g., Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Martin, Wiggs, Ungerleider, & Haxby, 1996; Spitzer, Kwong, Kennedy, Rosen, & Belliveau,

1995). Since picture naming is assumed to be mediated by semantic processes (see, e.g., Humphreys, Riddoch, & Quinlan, 1988), category-specific brain activations were taken as support for multiple semantic subsystems. In a study using positron-emission tomography (PET), Martin et al. observed that naming tools elicited a stronger activation than naming animals in an extended area of the left frontal lobe as well as in an area of the left temporal lobe. Conversely, naming animals activated an area in the left occipito-temporal region more strongly than did naming tools. The neuroanatomical locations of these category-specific areas were largely confirmed in a recent neuropsychological study with brain-damaged patients by Tranel, Damasio, and Damasio (1997). In that study, however, a relatively greater importance of the right-hemisphere regions for the processing of natural categories was observed.

Alternative Interpretations of Category-Specific Effects

The precise interpretation of category-specific effects in semantic memory tasks is still a matter of controversy. In particular, the relative contributions of semantic and perceptual factors to category-specific effects have been debated. According to a multiple-systems account, semantic knowledge associated with a given category is locally represented in the human brain to some extent. Hence, functionally and structurally distinct semantic subsystems are distinguished (Devlin, Gonnerman, Andersen, & Seidenberg, 1998; Farah & McClelland, 1991; Spitzer, 1998; Warrington & Shallice, 1984). For example, Warrington and her colleagues (Warrington & McCarthy, 1987; Warrington & Shallice, 1984) have proposed that category-specific deficits in brain-damaged patients emerge from a more fundamental distinction between visual and functional

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semantic knowledge. Their so-called sensory-functional hypothesis states that visual semantic knowledge is more important for identifying objects from natural categories than for objects from artifactual categories because they require a more fine grained differentiation between visual attributes. In contrast, functional semantic knowledge is supposed to be more relevant for objects from artifactual categories because the visual appearance of objects from a given artifactual category can vary considerably. However, artifactual objects are specifically designed to subserve a certain function (see Tranel, Logan, Frank, & Damasio, 1997, for a factor analysis of various variables obtained from natural and artifactual objects).

The multiple-systems account for category-specific effects has been criticized by Humphreys and colleagues (Humphreys & Riddoch, 1987; Lloyd-Jones & Humphreys, 1997a, 1997b). They have argued that category-specific effects do not necessarily imply multiple semantic systems and provide a *perceptual account* of category-specific effects. This perceptual account states that objects from natural categories have similar shapes and are therefore perceptually not differentiated from each other. For that reason, objects from natural categories are called *structurally similar*. Objects from artifactual categories, in contrast, have distinct shapes. They are therefore perceptually more differentiated and are considered to be *structurally dissimilar*. In the perceptual account, it is assumed that visual identification of structurally similar objects is more difficult than identification of structurally dissimilar objects.

Selective deficits in natural categories in brain-damaged patients are explained on the grounds of these perceptual differences; that is, the more difficult process of visual recognition of natural objects is more readily disturbed by any nonspecific damage to the structural representation and/or the semantic system. Selective deficits in artifactual categories are assumed to arise from damage to representations of functional object knowledge. In that respect, the perceptual and the multiple-systems accounts provide similar interpretations.

In particular, early reports of category-specific semantic memory impairments in natural categories have been criticized as visual complexity, familiarity, and name frequency of the stimuli were not properly controlled (Humphreys & Riddoch, 1987). Accordingly, deficits in natural categories disappeared in some patients when these variables were taken into account (Funnell & Sheridan, 1992; Parkin & Stewart, 1993). However, in more recent studies that were explicitly controlled for these factors patients still exhibited a deficit in natural categories (e.g., Farah, McMullen, & Meyer, 1991; Kurbat, 1997). Furthermore, selective deficits in natural categories are not only reported in the visual, but likewise in other sensory as well as in the verbal input modality (e.g., Sheridan & Humphreys, 1993). Hence, category-specific semantic memory impairments cannot be simply attributed to perceptual difficulty.

Yet, there is recent evidence that perceptual sources still contribute to category-specific effects even when stimuli were controlled for name frequency, visual complexity, and familiarity. Studies with healthy subjects showed that pictures with objects from natural categories took longer to be named than did objects from artifactual categories (Lloyd-Jones & Humphreys, 1997a, 1997b). In a regression analysis, "perceptual feature overlap" was the most important predictor for naming latencies (Lloyd-Jones & Humphreys 1997b). Furthermore, naming of objects from natural but not from artifactual categories was facilitated by surface details such as texture and color (Price & Humphreys, 1989; Tanaka & Presnell, 1999). These findings suggest that visual features are more important for the processing of natural than of artifactual categories, probably because natural categories show a greater perceptual similarity.

Electrophysiological Correlates of Perceptual and Semantic Processing

Recordings of time-locked brain electrical activity have been frequently used to uncover structure and processes underlying task performance (Rugg & Coles, 1995). In contrast to behavioral measures, the ERP method allows the on-line analysis of cognitive processes with a temporal resolution in the range of milliseconds and conveys information about their neural substrates. ERPs have been successfully applied to examine semantic processing in numerous studies (for an overview, see Kutas & Van Petten, 1994). For instance, the N400 ERP-component—that is, a negative deflection in the ERP peaking at about 400 msec after stimulus presentation—has been widely used as an electrophysiological index of *semantic processing* (Kutas & Hillyard, 1980). The N400 has been shown to be specifically sensitive to semantic deviations (Kutas & Hillyard, 1980, 1983). Furthermore, the scalp distribution of the N400 appears to be sensitive to structural aspects of semantic memory since it differs between concrete and abstract words (Kounios & Holcomb, 1994). Using ERPs, it was also possible to differentiate the semantic representations of action verbs and nouns evoking visual associations (Dehaene, 1995; Pulvermüller, Preissl, Lutzenberger, & Birbaumer, 1996).

ERPs can also be applied to distinguish between perceptual and semantic processes in object categorization. In a recent study, Tanaka, Luu, Weisbrod, and Kiefer (1999) observed that subordinate categorizations (e.g., poodle) of a depicted object elicited a larger N1 than basic level (e.g., dog) or superordinate categorizations (e.g., animal) starting at about 150 msec after target presentation. The visual N1 ERP component, an early negative deflection in the ERP, reflects *perceptual processing* and is enlarged when attention is paid to visual stimuli (Mangun & Hillyard, 1991). This ERP effect supports previous cognitive studies suggesting that subordinate categorization requires extended perceptual processing (Jolicœur,

Gluck, & Kosslyn, 1984). In contrast, Tanaka et al. found a frontal ERP effect related to superordinate relative to basic-level categorizations starting at about 300 msec after target presentation. Since frontal ERP effects reflecting *semantic processing* have been described in several studies (Kiefer, Weisbrod, Kern, Maier, & Spitzer, 1998; Snyder, Abdullaev, Posner, & Raichle, 1995), this observation is consistent with the assumption that superordinate categorization requires additional semantic processing (Jolicœur et al., 1984).

The Present Study

The present study was designed to dissociate perceptual and semantic sources underlying category-specific effects in neurologically intact subjects. ERPs recorded during task performance were used for tracking the time course of cognitive processes involved in object categorization. ERPs to natural and artifactual categories were assessed in a superordinate categorization task with pictures and object names as target stimuli. Contributions of perceptual and semantic processes can be distinguished by their corresponding ERP events, as modulated by natural and artifactual categories.

ERP effects related to perceptual processing are observed relatively early after stimulus presentation in the N1 window (between 100 and 200 msec) at posterior electrode sites. As noted, due to their greater perceptual similarity, visual information presumably plays a more important role for the categorization of objects from natural than from artifactual categories. According to this assumption, the visual N1 ERP component should be enlarged to natural categories. In contrast, ERP effects related to semantic processing are usually obtained somewhat later in the N400 time window between 200 and 500 msec after target presentation (Kutas & Hillyard, 1980). In numerous studies, the N400 has been shown to be sensitive for semantic congruency (i.e., a greater N400 for words or pictures that violate the semantic context in comparison with semantically congruent stimuli). More important for the present study, category-specific ERP differences in the N400 window are most likely related to category-specific access to semantic memory. Given what is known about category-specific semantic memory organization from neuropsychological and neuroimaging studies, artifactual and natural categories should differentially modulate the N400 ERP component at fronto-central and occipito-temporal electrode sites.

The systematic variation of object category and target modality further helps to dissociate perceptual and semantic sources. If category-specific effects reflect semantic memory organization rather than merely differences in perceptual processing, they should be observed with pictorial as well as with verbal stimuli. In contrast, category-specific effects confined to pictorial stimuli are most likely due to perceptual differences.

EXPERIMENTS 1 AND 2

In the first experiment, subjects had to indicate whether or not a given superordinate category name (e.g., "animal") is appropriate to a target object (e.g., cat). This standard paradigm has several limitations. First, manipulation of target modality is confounded with the absence or presence of a modality switch between category probe and target object. Second, the verbal category label may have encouraged the subjects to adopt a verbal strategy even in the pictorial modality. For these reasons, a second experiment was conducted in which the target stimuli (pictures and words) and procedure were identical to those of Experiment 1, but the category probe was presented pictorially in form of an object pair (e.g., zucchini and kohlrabi as probe for the category vegetable; see Figure 1). The rationale for using an object pair instead of a single object as category probe was that a pair represents the entire conceptual and perceptual range of a given superordinate category to a greater extent than a single object does.

Method

Since both experiments were basically the same regarding the experimental design and procedures, they are described together in the following method section, with any methodological differences noted.

Subjects

Twenty-five right-handed University of Heidelberg students participated in Experiments 1 and 2, respectively. All of the subjects participated in only one experiment and gave an informed consent. Participation in the experiments was voluntary and not paid. Hand dominance was assessed with a translated German version of the Edinburgh Inventory (Oldfield, 1971). Subjects were native German speakers with no neurological or psychiatric disorder and normal or corrected-to-normal vision. In each experiment, data of 5 subjects had to be excluded from analysis because of excessive artifacts in the EEG recordings (less than a minimum of 60% artifact-free trials). In Experiment 1, the remaining 20 subjects (10 male/10 female) had an average age of 26.4 years (range = 22–34). In Experiment 2, average age of the 20 included subjects (10 male/10 female) was 24.5 years (range = 19–29).

Materials

Experiment 1 stimuli consisted of a superordinate category name as probe and a target object (Figure 1). One hundred sixty color pictures of common objects and 160 corresponding object names served as targets. Half the objects belonged to artifactual categories (20 items from the categories of tools, furniture, transportation, and musical instruments, respectively) and the other half were from natural categories (20 instances from the categories of animals, plants, fruits, and vegetables, respectively). These categories were most frequently used in previous studies (e.g., Spitzer et al., 1995; Warrington & McCarthy, 1987). Pictures were digitized mainly from *The Macmillan Visual Dictionary* (Corbeil & Archambault, 1994) and adjusted in size. The objects were depicted in a canonical view against a white background.

For the selection of the target objects, two pretests were run. In the first pretest ($n = 15$), object names for the verbal condition and naming latencies for the pictures as an index for picture recognition difficulty were obtained. For each picture, mean naming latency

Figure 1. Temporal sequence of events in one trial of the superordinate categorization task. The example in the top row is an instance of a category name/target object pairing as used in Experiment 1 (congruent condition). The bottom row exemplifies a category picture–target object pairing as used in Experiment 2 (incongruent condition).

was calculated and the most frequent object name was determined, which was subsequently used in the main experiments. Only objects that could be correctly named by at least 70% of the subjects were included in the final stimulus set. In the second pretest, typicality ratings for the objects were obtained from a new sample of 20 subjects.

Stimuli were selected so that target objects from natural and artificial categories did not differ from each other significantly in typicality [natural, 4.65; artificial, 4.56; $t(1,158) = 1.221$] and naming latency [natural, 1,215 msec; artificial, 1,186; $t(1,158) = .972$] as well as in word length [natural, 6.9 letters; artificial, 7.5; $t(1,158) = -1.350$] and in word frequency [according to Ruoff, 1990; natural, 8.08 per 500,000; artificial, 9.53 per 500,000; $t(1,158) = -.409$] of the object names. Categories were also equated in terms of the average width [natural, 6.4 cm; artificial, 6.2 cm; $t(1,158) = .492$] and height [natural, 5.7 cm; artificial, 6.2 cm; $t(1,158) = .804$] of the pictures as well as the width [natural, 4.8 cm; artificial, 5.2 cm; $t(1,158) = -1.204$] and the height (1.7 cm for both categories) of the object names. At a distance of 95 cm, the viewing angle for the pictorial stimuli subtended on average 3.8° horizontally and 3.4° vertically, and for the verbal stimuli, 3° horizontally and 1° vertically. The category labels had an average width of 6.2 cm and an average height of 1.7 cm (viewing angle, 3.7° horizontally, 1° vertically). Since natural and artificial categories were initially matched for name frequency, naming latency, and typicality, but not for complexity and familiarity of the pictures, both variables were measured post hoc following the instructions of Snodgrass and Vanderwart (1980) in a group of 20 new subjects. Mean differ-

ences in these variables were small [complexity, artificial = 2.8 vs. natural = 2.5, $t(158) = 2.067$, $p < .05$; familiarity, artificial = 2.8 vs. natural = 3.1, $t(158) = 3.9$, $p < .001$], but statistically reliable.

In half the trials, category–target object pairings were semantically congruent; that is, the object was a member of the specified category (e.g., animal–cat), and in the other half they were semantically incongruent. Semantic congruency and kind of category (natural or artificial) were varied orthogonally. This was achieved by re-grouping congruent category–target object pairings only within a given kind of category to obtain items for the incongruent condition (e.g., animal–rose). All category–object pairs were divided into two stimulus lists in such a way that each object occurred in one list in the congruent and in the other list in the incongruent condition. Each subject saw both stimulus lists. However, one list was presented with targets in the pictorial and the second list with targets in the verbal modality. The assignment of the lists to the different target modalities and the presentation order of the modalities was counter-balanced across subjects. As a result, each object occurred with the same frequency in the congruent and incongruent conditions in both the pictorial and the verbal modalities. This procedure yielded a $2 \times 2 \times 2$ completely crossed factorial design with modality, category, and semantic congruency as independent variables. In total, subjects received 40 trials for each of the eight experimental conditions.

The only change in the second experiment concerned the modality of the presented category. Instead of the category names, categories were probed by a pair of depicted objects (Figure 1). Throughout the experiment, the same pair of objects was used for a given category. The categories were visualized by the following pairs of

objects, which were not used as targets: transportation (cabriolet, subway), tools (crowbar, shovel), furniture (folding chair, kidney-shaped table), musical instrument (mouth organ, keyboard), fruit (cranberry, apricot), vegetable (zucchini, kohlrabi), plants (maple, deadnettle), animal (duck, sheep). The object pairs were selected so that visual similarity within one pair was minimized and so that a broad range of category instances were represented. The pictures were adjusted in size and were placed pairwise in the lower left and in the upper right corner of the category-specifying picture. These pictures were 9.7 cm in length and 6.4 cm in height (viewing angle, 5.8° horizontal, 3.8° vertical). A pretest with 10 new subjects showed that the category pictures probed the intended categories unequivocally.

Procedure

In Experiment 1, subjects were seated in front of a computer screen with their chins positioned on a chinrest in a dimly lit electrically shielded room. All stimuli were displayed in the center of a computer screen synchronous with the screen refresh rate. Each trial started with the presentation of a fixation cross for 750 msec that was replaced by a superordinate category name for 300 msec. After an interstimulus interval (ISI) of 600 msec the target stimulus was displayed. The target remained on the screen until the subject responded. It disappeared automatically after 3,000 msec if there was no response, and the trial was counted as an error. Reaction times (RTs) to the target stimuli as well as the correctness of the response were recorded. Following the subject's response, three stars were displayed, which prompted the subject to initialize the subsequent trial with a mouse click (see also Figure 1). Subjects were presented with a category name and thereafter with an object. They were requested to decide as quickly and as accurately as possible whether the target object was a member of the previously presented category or not. Subjects responded with their right hands using the index finger for yes responses (left mouse button) and the middle finger for no responses (right mouse button). Subjects were also instructed to refrain from moving and blinking. Picture and word targets were presented in separate blocks. Within the blocks, the order of the category–target object pairs was randomized. Before the main experiment, a practice experiment consisting of 32 trials was run. A second practice experiment with 16 new trials was run before the second block when the target modality was changed. In both training phases, feedback on the correctness of the response was given. In the main experiment, subjects did not receive feedback regarding their performance. The entire experimental session required about 2 h to complete. In Experiment 2, experimental procedure was identical to that of Experiment 1 except that, instead of the verbal category labels, category pictures were shown. At the beginning of the experiment, subjects were familiarized with the category pictures printed on a sheet of paper. The categories were never named by the experimenter.

ERP Recording and Signal Extraction

Scalp voltages were collected using a 64-channel Geodesic Sensor Net (Tucker, 1993). The net consists of 66 sintered Ag/AgCl electrodes, which occupy the vertices of a triangular mesh of elastic line. This ensures their regular repartition on the surface of the scalp with a spacing of about 4 cm (see Figure 2). A right inferior occipital electrode was connected to the ground, and the vertex electrode was used as reference. Eye movements were monitored with supra- and infra-orbital electrodes and with electrodes on the external canthi. Electrode impedance was maintained below 20 k Ω for all recordings. Electrical signals were amplified with Synamps amplifiers (low-pass filter = 70 Hz, 24-dB/octave attenuation; 50-Hz notch filter). Scalp voltages were continuously recorded, digitized by a microcomputer at a sampling rate of 250 Hz, and stored on the hard disk for off-line analysis. The continuous EEG was seg-

Figure 2. Electrode locations on the Geodesic net. Each number represents a recording site. A line indexes the groups of bilateral pairs of electrodes selected for statistical analysis.

mented in epochs starting 150 msec before the onset of the target and lasting until 900 msec after its onset.

The EEG epochs were digitally low-pass filtered with an upper cutoff at 16 Hz using a two-pole double Butterworth filter and were aligned to the 150-msec baseline before the onset of the target. EEG epochs were examined, and all trials contaminated with ocular or movement artifacts were discarded. Trials with correct responses were averaged separately for conditions, synchronous to the onset of the target. On average, individual subject averages were based on 32.1 trials (range = 21–40). The number of trials included in the averages did not differ significantly between conditions [$F(7,133) = 1.341$, $MS_e = 10.482$, $p < .24$]. The average-reference transform was applied to obtain a reference-independent estimation of scalp voltage (Bertrand, Perrin, & Pernier, 1985), and the reconstructed vertex reference was added to the data, resulting in a total of 65 data channels. The average-reference transformation has been shown to be useful for topographic ERP analysis in previous studies (e.g., Kiefer et al., 1998).

Statistical Analysis

Scalp voltage was analyzed statistically at bilateral pairs of electrodes in specific time windows. To restrict the number of statistical comparisons, electrodes were selected a priori in several scalp regions of interest according to theoretical predictions. Two time windows were determined according to the major ERP features of theoretical interest observed in the data set: (1) the visual N1 with a maximum over posterior areas and (2) the centro-parietal N400. In both experiments, the N1 was analyzed in the time window of 166–206 msec and the N400 in the time window of 370–520 msec post-target. Mean voltages were computed for each time window and for selected pairs of bilateral electrodes in four scalp regions (Figure 2): fronto-central (16/53, 10/58), centro-parietal (28/41, 17/42, 5/54), occipito-temporal (33/40, 27/45, 25/46), and inferior temporo-occipital (30/50, 31/47). ERPs in the N1 time window were analyzed at inferior temporo-occipital electrodes because early perceptual effects on ERPs were expected in this scalp region (Tanaka et al., 1999). ERPs in the N400 window were assessed at fronto-central, centro-parietal, and occipito-temporal electrodes, since the

N400 is largest in these regions (Kutas & Hillyard, 1980). Furthermore, categories are expected to elicit differential ERP waves, particularly at fronto-central and occipito-temporal electrodes (Dehaene, 1995; Pulvermüller et al., 1996).

To reduce complexity of statistical analysis, voltages were averaged across electrode sites in each scalp region of interest. Separate repeated measures analyses of variance (ANOVAs) were performed for picture and word targets on mean voltage of each time window with category, congruency, and hemisphere as factors. Mean differences between conditions were subsequently assessed using Newman-Keuls tests. When appropriate, degrees of freedom were adjusted according to the method of Greenhouse-Geisser, and only corrected significance levels are reported. The level of significance testing was $p = .05$.

Results

Experiment 1: Category Names

Behavioral results. Repeated measures ANOVAs were carried out on RT to the targets and on error rate (ER), with modality, category, and congruency as factors. RT analysis was based on mean RT of the correct responses per condition. Responses longer than twice the individual mean were rejected as outliers (.76% of the data set). Analysis revealed that picture targets were categorized faster than word targets [main effect of modality, $F(1,19) = 4.488$, $MS_e = 24,124.8$, $p < .05$], and reactions to congruent targets were faster than to incongruent targets [main effect of congruency, $F(1,19) = 33.183$, $MS_e = 4,624.4$, $p < .0001$]. Moreover, category interacted with congruency [$F(1,19) = 17.232$, $MS_e = 756.3$, $p < .001$]. Newman-Keuls tests revealed that objects from natural categories were verified faster than objects from artificial categories when category and target were congruent. In the incongruent condition, RT between categories was not significantly different. Modality interacted with neither category nor congruency ($F < 1$). Hence, category and congruency

affected verification latencies largely independently of modality (Figure 3).

Analysis of ER yielded a main effect of category [$F(1,19) = 7.805$, $MS_e = 6.7$, $p < .01$] that was qualified by a category $\times$ congruency interaction [$F(1,19) = 26.482$, $MS_e = 27.3$, $p < .0001$]. Post hoc tests indicated that in the congruent condition, more errors were made for artifactual than for natural categories. In the incongruent condition, ER was higher for natural than for artifactual categories (Figure 3). The factor modality was not significant and it did not interact with any other factor ($F < 1$).

Electrophysiological data. In all conditions, presentation of the target elicited a visual P1 ERP component at about 130 msec posttarget onset followed by a visual N1 at about 180 msec posttarget onset (Figure 4). These early components were largest over the posterior part of the head at inferior temporal and occipital electrodes, thus roughly over the visual cortices. Both ERP components reflect perceptual processing of visual stimuli (Mangun & Hillyard, 1991). In the N1 time window, category-specific differences emerged only in the pictorial modality. Natural categories elicited a larger visual N1 than artifactual categories. In the subsequent part of the recording epoch a broad negative deflection was observed at centro-parietal electrodes (around the vertex—the middle of the head), at fronto-central electrodes (roughly over the motor cortices), and also over the back of the head at occipito-temporal electrodes. This negative deflection was larger to incongruent than to congruent trials and peaked at about 400 msec after target presentation. According to its latency, topography, and sensitivity to semantic congruity, this deflection was identified as an N400 ERP component (Kutas & Hillyard, 1980). The N400 was partially overlapping with a posterior positivity that was more rapidly rising for congruent trials and that is known as the “late positive complex” (LPC). In the N400 time window, ERPs to natural and artifactual categories diverged in both input modalities. Natural categories elicited a less negative potential than artifactual categories over the right hemisphere, in particular at right occipito-temporal electrodes—that is, over posterior parts of the head superior to the electrodes at which the N1 effect was obtained. In the pictorial modality, potentials to artifactual categories were less negative than to natural categories at left fronto-central electrodes.¹ Thus, category-specific ERP differences were observed that were at least in part comparable for both modalities.

Statistical analysis of the ERP data focused on two time windows of interest: (1) the early time window (visual N1) and (2) the late time window (N400). (For the rationale of time window and electrode selection, see the Method section.) In order to reduce complexity of the Results section, main effects of hemisphere that are not of theoretical interest are not reported.

Figure 3. Mean RTs ($n = 20$) and error rates (ERs) in the supordinate verification task of Experiment 1 for picture and word targets as a function of category and semantic congruency (lines = RT; bars = ER). The error bars depicted in the present and the upcoming figures indicate the standard errors of the mean of each condition.

Figure 4. Selected ERP waveforms of average-referenced grand-averaged data ($n = 20$) for picture and word targets from Experiment 1 as a function of object category and semantic congruency. Potentials are collapsed across electrode sites within each scalp region. For the location of the electrodes refer to Figure 2. The long vertical line indicates the onset of the target. In this and the following figures, negative potentials are plotted downward and positive potentials upward. The small closed arrows indicate the early category-specific ERP effect on the visual N1. The large arrows refer to late category-specific effects (N400): Closed arrowheads indicate scalp regions where natural categories elicited a less negative potential than artifactual categories (i.e., natural categories showed a decrement in N400 amplitude). Open arrowheads refer to regions where artifactual categories elicited a less negative potential than natural categories.

Figure 5. Mean voltages (average-referenced data; $n = 20$) from Experiment 1 for the late time window (N400; 370–520 msec) at selected electrode groups (collapsed across electrode sites) as a function of object category and hemisphere in the pictorial and verbal target modality. An asterisk indicates significant effects between categories in the ANOVAs. Note a less negative potential to artifactual categories in the fronto-central region, particularly over the left hemisphere. ERPs to natural categories were less negative over the right hemisphere, in particular over the occipito-temporal region.

torial modality, differences between categories were observed [main effect category, $F(1,19) = 30.503$, $MS_e = 766.5$, $p < .0001$]. ERPs to natural categories were more negative than to artifactual categories; that is, visual N1 was larger to natural than to artifactual categories. In the verbal modality no comparable effect was obtained (Figure 4).

Late time window (N400). In the N400 time window (370–520 msec after target presentation), ERPs were assessed at fronto-central, centro-parietal, and occipito-

temporal electrodes. The results of these analyses are reported separately for each scalp region (Figures 4 and 5).

1. *Fronto-central:* Congruency affected ERPs in both the pictorial and verbal modalities [picture, $F(1,19) = 23.410$, $MS_e = 956.7$, $p < .001$; word, $F(1,19) = 25.373$, $MS_e = 1,783.0$, $p < .0001$]. Incongruent targets were more negative than congruent targets. Hence, an N400 congruency effect was demonstrated for both picture and word targets. Moreover, in the pictorial modality, a hemisphere-specific effect of category was observed as indexed by a

category $\times$ hemisphere interaction [$F(1,19) = 13.041$, $MS_e = 704.2$, $p < .01$]. Post hoc tests revealed that artifactual categories were less negative than natural categories over the left hemisphere. As can be seen in Figure 4, artifactual categories were developing a positive shift relative to natural categories, thereby reducing the N400. Over the right hemisphere, the opposite voltage pattern was observed: Natural categories were less negative than artifactual categories.

2. Centro-parietal: Congruency affected ERPs in the pictorial and verbal conditions [picture, $F(1,19) = 17.664$, $MS_e = 2,371.6$, $p < .001$; word, $F(1,19) = 44.069$, $MS_e = 2,289.9$, $p < .0001$]. ERPs to incongruent targets were more negative than those to congruent targets. Hence, an N400 congruency effect was also obtained over the centro-parietal area. In addition, category-specific differences were observed. In the pictorial modality, a main effect of category [$F(1,19) = 6.171$, $MS_e = 1,703.3$, $p < .05$] was qualified by a category $\times$ congruency interaction [$F(1,19) = 12.467$, $MS_e = 1,625.5$, $p < .01$]. Post hoc tests revealed that congruent and incongruent targets differed significantly from each other in artifactual, but not in natural, categories. Hence, an N400 congruency effect was obtained only in artifactual categories. Furthermore, it turned out that differences between categories were confined to the incongruent condition. A category $\times$ hemisphere interaction [$F(1,19) = 8.183$, $MS_e = 560.9$, $p < .05$] indicated a less negative potential over the right centro-parietal region for natural than for artifactual categories. In the verbal modality, a category $\times$ congruency $\times$ hemisphere interaction was obtained [$F(1,19) = 6.177$, $MS_e = 269.8$, $p < .05$]. The congruency effect for artifactual categories was larger than for natural categories over the right hemisphere. Post hoc tests showed that ERP differences between congruent and incongruent targets were reliable over both hemispheres in natural as well as in artifactual categories. As in the pictorial modality, category-specific differences were confined to the incongruent condition.

3. Occipito-temporal: At occipito-temporal electrodes, category-specific effects were also observed in both the pictorial and verbal modalities. In the pictorial modality, a main effect of category was obtained [$F(1,19) = 8.376$, $MS_e = 2,668.7$, $p < .01$] that was modified by a category $\times$ hemisphere interaction [$F(1,19) = 8.793$, $MS_e = 1,015.0$, $p < .01$]. Likewise, the category $\times$ hemisphere interaction was also significant in the verbal modality [$F(1,19) = 5.198$, $MS_e = 770.3$, $p < .05$]. Post hoc tests showed that ERPs to natural categories were less negative than to artifactual categories over right occipito-temporal areas. Categories did not differ from each other significantly over the corresponding left hemisphere region.

Summary of the ERP results. In the early time window (visual N1), category affected ERPs only in the pictorial modality. Natural categories elicited a greater N1 than artifactual categories. In the late time window (N400), category-specific ERP differences emerged in both modalities at right-hemisphere electrodes, in particular

over occipito-temporal and centro-parietal regions. Natural categories elicited a less negative potential than artifactual categories. In the pictorial modality, category-specific differences were also obtained at fronto-central electrodes: Over the left hemisphere, artifactual categories elicited relative to natural categories a less negative potential. Over the right hemisphere the opposite pattern was observed—that is, a less negative potential to natural categories. Hence, categories affected the N400 ERP component differentially. Finally, a N400 congruency effect was observed at fronto-central and centro-parietal electrodes (i.e., a more negative potential to incongruent than to congruent targets). The N400 congruency effect was larger in artifactual than in natural categories at centro-parietal electrodes. In the verbal modality, a corresponding category-specific difference in the N400 congruency effect was confined to the right hemisphere.

Experiment 2: Category Pictures

Behavioral results. Analysis of verification latencies was based on mean RT of the correct responses per condition. Responses longer than twice the individual mean were rejected as outliers (.57% of the data set). A repeated measures ANOVA with modality, category, and semantic congruency as factors showed main effects of modality [$F(1,19) = 5.920$, $MS_e = 12,517.2$, $p < .05$] and congruency [$F(1,19) = 22.862$, $MS_e = 4,092.1$, $p < .001$]. Responses to picture targets were faster than to word targets, and the acceptance of a congruent target as a member of a category occurred faster than the rejection of an incongruent target (Figure 6). Furthermore, a modality $\times$ category interaction [$F(1,19) = 17.056$, $MS_e = 1,012.8$, $p < .001$] indicated that category-specific RT effects differed between modalities. Post hoc tests revealed that RT differences between categories were restricted to the pic-

Figure 6. Mean RTs and error rates (ERs; $n = 20$) in the superordinate verification task of Experiment 2 for picture and word targets as a function of category and semantic congruency (lines = RT; bars = ER).

torial modality. Verification latencies were shorter to natural than to artifactual categories. In the verbal modality, mean differences were not statistically reliable. A marginally significant triple interaction of modality $\times$ category $\times$ congruency [$F(1,19) = 3.819, MS_e = 844.9, p < .065$] suggests that category-specific RT differences observed in the pictorial modality were larger in the congruent than in the incongruent condition. These modality- and category-specific effects contrast the findings of Experiment 1, in which category-specific differences occurred regardless of input modality. Inspection of Figures 3 and 6 reveals another major difference between the experiments. The overall RT in Experiment 2 was about 100 msec faster than in Experiment 1. As can be seen, this was a general effect independent of target modality and category.

ERs were also subjected to a repeated measures ANOVA with modality, category, and congruency as factors. In this analysis, marginally significant interactions for modality $\times$ category [$F(1,19) = 4.104, MS_e = 19.6, p < .057$] and modality $\times$ category $\times$ congruency [$F(1,19) = 4.089, MS_e = 19.9, p < .057$] were observed. The triple interaction indicated that the ER pattern was different for picture and word targets. In the pictorial modality, ERs were higher when a congruent object had to be accepted as a member of an artifactual category than as that of a natural category. In contrast, subjects were less accurate in their rejections of an incongruent object from a natural category relative to an incongruent object from an artifactual category. Hence, there was a particular difficulty in accepting congruent objects from artifactual categories and in rejecting incongruent objects from natural categories. In the verbal modality, ER was higher for natural than for artifactual categories (Figure 6).

Electrophysiological results. Presentation of the target stimuli elicited ERP events similar to those in Experiment 1: the early sensory components P1 and N1 over inferior occipital and inferior temporal areas and the later N400 as well as a broad parietal and occipito-temporal positivity (LPC). The ERP wave forms in Figure 7 show a pattern of early and late category effects similar to that observed in Experiment 1—an early effect on the visual N1 confined to the pictorial modality (i.e., a larger N1 amplitude to natural categories) and later category-specific differences in both modalities, most pronounced at fronto-central and occipito-temporal electrodes. As in Experiment 1, ERPs were statistically analyzed in the early time window (N1) and the late time window (N400).

Early time window (N1). In this time window, scalp voltages were analyzed at inferior temporo-occipital electrodes (see also Figure 7). In the pictorial modality, a significant effect of category was obtained [$F(1,19) = 13.931, MS_e = 20,692.0, p < .001$]: Natural categories elicited a greater N1 than artifactual categories. There was also a marginal effect of congruency [$F(1,19) = 3.733, MS_e = 15,410.9, p < .07$]. ERPs to congruent targets were more negative than to incongruent targets. In the

verbal condition, category-specific differences in N1 amplitude were not statistically reliable.

Late window (N400). In this time window, ERPs were analyzed at fronto-central, centro-parietal, and occipito-temporal electrodes (Figures 7 and 8).

1. *Fronto-central:* In both modalities, incongruent targets elicited a more negative potential than congruent targets, as indexed by a main effect of congruency [picture, $F(1,19) = 25.476, MS_e = 2,098.5, p < .0001$; word, $F(1,19) = 32.384, MS_e = 2,124.8, p < .0001$]. Hence, an N400 congruency effect was obtained. Furthermore, category-specific differences were observed in both modalities. ERPs to artifactual categories were less negative than ERPs to natural categories [main effect category, picture, $F(1,19) = 12.260, MS_e = 855.5, p < .01$; word, $F(1,19) = 6.788, MS_e = 1,099.4, p < .05$]. Unlike in Experiment 1, comparable effects were observed in both modalities. In the pictorial modality, the category $\times$ congruency [$F(1,19) = 13.439, MS_e = 581.0, p < .01$] interaction indicates that the congruency effect was larger in artifactual than in natural categories. Post hoc tests showed that mean differences between congruent and incongruent targets were reliable in both categories. Furthermore, categories significantly differed from each other only in the congruent condition: Artifactual categories elicited a less negative potential than natural categories. In the verbal modality, a corresponding category $\times$ congruency interaction was only marginally significant [$F(1,19) = 3.979, MS_e = 1,283.5, p < .06$]. In the pictorial modality, the category-specific effect differed between hemispheres (interaction category $\times$ hemisphere, $F(1,19) = 7.615, MS_e = 399.5, p < .05$). Post hoc tests revealed that the voltage difference between categories was reliable only over the left hemisphere (i.e., a less negative potential to artifactual than to natural categories).

2. *Centro-parietal:* At centro-parietal electrodes, incongruent targets elicited a larger N400 component than congruent targets in all conditions [main effect congruency, picture, $F(1,19) = 53.793, MS_e = 2,791.9, p < .0001$; word, $F(1,19) = 51.010, MS_e = 4,227.38, p < .0001$]. Moreover, category-specific differences were observed. The congruency effect was larger for artifactual than for natural categories in both modalities, as indicated by a category $\times$ congruency interaction [picture, $F(1,19) = 56.661, MS_e = 436.3, p < .0001$; word, $F(1,19) = 4.447, MS_e = 1,686.4, p < .05$]. Post hoc tests showed that ERPs to congruent and incongruent targets differed significantly from each other in all conditions. In the pictorial modality, differences between categories were reliable in the congruent as well as in the incongruent condition; in the verbal modality, category-specific differences were restricted to congruent targets. In the congruent condition, artifactual categories were less negative than natural categories. In the incongruent condition, the opposite voltage pattern was found.

3. *Occipito-temporal:* A main effect of category was observed in both the pictorial and verbal modalities [pic-

Figure 7. Selected ERP waveforms of average-referenced grand-averaged data ($n = 20$) for picture and word targets from Experiment 2 as a function of object category and semantic congruency. Potentials are collapsed across electrode sites within each scalp region. The long vertical line indicates the onset of the target. The small closed arrows indicate the early category-specific ERP effect on the visual N1. The large arrows refer to late category-specific effects (N400): Closed arrowheads indicate scalp regions where natural categories elicited a less negative potential than artificial categories. Open arrowheads refer to regions where artificial categories elicited a less negative potential than natural categories.

Figure 8. Mean voltages (average-referenced data; $n = 20$) from Experiment 2 for the late time window (N400; 370–520 msec) at selected electrode groups (collapsed over electrode sites) as a function of object category and hemisphere in the pictorial and verbal target modality. *Significant effects between categories in the ANOVAs.

ture, $F(1,19) = 25.327$, $MS_e = 1,977.9$, $p < .0001$; word, $F(1,19) = 4.898$, $MS_e = 3,529$, $p < .05$]. Natural categories were associated with a less negative potential than artifactual categories. In the pictorial modality, a category $\times$ hemisphere interaction [$F(1,19) = 12.161$, $MS_e = 688.6$, $p < .01$] indicates that category-specific differences were larger over the right than over the left hemisphere. Post hoc tests showed that mean differences between categories were significant on either side. Finally, a category $\times$ congruency interaction [$F(1,19) = 14.569$,

$MS_e = 315.9$, $p < .01$] was significant: Category-specific differences were largest in the incongruent condition, but post hoc tests revealed reliable differences between categories in both the congruent and the incongruent conditions. In artifactual categories, incongruent targets elicited a more negative potential than congruent targets. Hence, an N400 congruency effect similar to that at centro-parietal electrodes was observed. In natural categories, the opposite pattern was obtained: Incongruent targets were less negative than congruent targets. In the verbal modal-

ity, a main effect of congruency was obtained [$F(1,19) = 11.460$, $MS_e = 2,399.6$, $p < .01$], showing that incongruent targets were more negative than congruent targets.

Summary of the ERP results. As in Experiment 1, category affected ERPs to picture targets, but not to word targets in the N1 time window: N1 amplitude was greater to natural than to artifactual categories. In the late time window, category-specific ERP effects over occipito-temporal and fronto-central areas were replicated. Natural categories elicited a less negative potential over occipito-temporal regions, whereas artifactual categories were less negative over fronto-central regions. Finally, a congruency effect on the N400 amplitude was obtained in all conditions. ERPs to incongruent targets were more negative than to congruent targets. As in Experiment 1, category interacted with congruency: The ERP difference between congruent and incongruent targets was larger for artifactual than for natural categories. At fronto-central and centro-parietal electrodes, categories predominantly differed in the congruent condition: Artifactual categories were less negative than natural categories. In the pictorial modality, categories diverged also in the incongruent condition at centro-parietal and occipito-temporal electrodes, at which natural categories were less negative than artifactual categories.

Discussion

Category-specific effects in semantic tasks have meanwhile been demonstrated in several behavioral (e.g., Lloyd-Jones & Humphreys, 1997a, 1997b), neuropsychological (e.g., Warrington & Shallice, 1984), electrophysiological (e.g., Dehaene, 1995), and neuroimaging (e.g., Martin et al., 1996) studies. The present study was designed to clarify the role of perceptual and semantic sources underlying category-specific effects. ERPs to natural and artifactual categories were recorded in different input modalities. If category-specific effects have perceptual sources, they should be confined to the pictorial modality. In contrast, if category-specific effects mirror semantic memory organization, they should be observed in both modalities.

The results of the experiments suggest that both sources, perceptual and semantic, contribute to category-specific effects in object categorization. Early ERP differences between artifactual and natural categories (about 160–200 msec) were restricted to the pictorial modality. Later in the recording epoch (between about 300 and 500 msec), category-specific ERP effects were obtained with both pictorial and verbal target stimuli. The late effects support the notion that the semantic memory system reflects the distinction between natural and artifactual categories in some respect. In the upcoming sections of the discussion, we first focus on the behavioral data and thereafter on the ERP effects in the early and the late time windows.

Behavioral Data

In both experiments, verification latencies were shorter for pictures than for words. Such a superiority of pictorial

stimuli over words in categorization tasks has been described in several studies (e.g., Bajo, 1988; Potter & Faulconer, 1975). It has been suggested that access to semantic memory is faster with pictures than with words. Despite this general difference in response latencies, the effects of congruency and category on RT (and ER) were strikingly similar for both modalities in Experiment 1 (verbal category probe). Objects from natural categories were accepted faster as a member of a category than objects from artifactual categories in both the pictorial and verbal modalities.

The present RT results are in line with a study by Price and Humphreys (1989) that also yielded an advantage for natural categories in object categorization (living/nonliving decision). The observation of faster responses to natural than to artifactual categories clearly contrasts with performance in naming tasks and in categorization tasks with highly similar contrast categories (e.g., fruit vs. vegetable) in which objects from natural categories are responded to more slowly than objects from artifactual categories (Lloyd-Jones & Humphreys, 1997a, 1997b). Possibly, members of natural categories are identified more slowly than members of artifactual categories when categorical decisions require fine-grained distinctions between competing alternatives. In contrast, natural categories are processed faster than artifacts when only broad distinctions between categories have to be made. Recently, Devlin et al. (1998) have suggested that artifactual and natural categories differ in the “informativeness or distinctiveness of semantic features” (which is greater in artifactual categories) and in the “intercorrelation of features” (which is greater in natural categories). Accordingly, categories with low informativeness of features (i.e., natural categories that comprise exemplars with many shared features) allow faster and more accurate verifications of category membership relative to categories with high informativeness of features (i.e., artifactual categories that include exemplars with few shared features). At the same time, rejections of objects that do not belong to the category (incongruent targets) are more difficult when features are highly intercorrelated. This assumption is also consistent with the distribution of errors in the present verification task. In artifactual categories, subjects made more errors with congruent than with incongruent targets, whereas in natural categories the opposite pattern was found.

Pictures from artifactual categories used in the present study were somewhat more complex and less familiar than those of natural categories. Therefore, it cannot be completely ruled out that natural categories were perceptually somewhat easier to process than artifacts. However, differences in complexity and familiarity cannot account for category-specific RT effects in the verbal modality and for the ERP effects discussed below (see also Lloyd-Jones & Humphreys, 1997b).

In Experiment 2, in which the category probe was presented pictorially, category-specific RT differences like those observed in Experiment 1 were observed for pic-

tures, but not for words (although category-specific ERP effects were still obtained for words). The latter finding is problematic for the multiple-systems account and favors a purely perceptual view of category-specific effects. However, a purely perceptual account could accommodate neither the behavioral findings from Experiment 1 nor the category-specific ERP effects in both experiments. It should be noted that the overall RT level in Experiment 2 was about 100 msec faster than in Experiment 1, suggesting that a pictorial category probe facilitates categorization (since there was also an associated increase of error rates in some conditions in Experiment 2 relative to Experiment 1, a speed-accuracy tradeoff cannot be entirely ruled out). It is possible that response speed affects category-specific processing more with verbal than with pictorial stimuli. On the grounds of the present data it is not possible to completely clarify the reasons for this unexpected result, but the greater stability of category-specific RT effects in the pictorial modality supports the notion of perceptual sources contributing to category-specific effects.

Early ERP Effects

In the early time window (between 160 and 200 msec after target onset), objects from natural categories elicited a greater N1 ERP component than objects from artifactual categories. This effect was present for pictorial but not for verbal targets (for a similar ERP effect, see Thorpe, Fize, & Marlot, 1996). It is well established in ERP research that the N1 reflects visual perceptual processing and that N1 amplitude is enhanced when attention is directed to visual stimuli (Mangun & Hillyard, 1991). Likewise, in the Tanaka et al. (1999) study, subordinate object categorizations (e.g., poodle) requiring more elaborate perceptual processing were associated with a greater N1 deflection than basic-level (e.g., dog) or superordinate categorizations (e.g., animal).

Hence, the greater visual N1 to natural categories supports the assumption of the perceptual account that perceptual information plays a more important role in the processing of natural than of artifactual categories (Lloyd-Jones & Humphreys, 1997a, 1997b). The present ERP results render it unlikely that picture complexity and familiarity are the relevant perceptual variables underlying this effect, since pictures from natural categories were rated slightly *less* complex and *more* familiar than artifactual categories. Therefore, if familiarity and complexity were modulating N1 amplitude, we would expect a larger N1 to artifactual categories. However, the opposite ERP pattern, a larger N1 to natural categories, was observed in the present experiments.

Presumably, the greater intracategorical perceptual similarity of objects from natural than from artifactual categories is the relevant factor for the present perceptual category-specific effect (Lloyd-Jones & Humphreys, 1997a, 1997b; Tranel, Logan, et al., 1997). There are three

possibilities for how perceptual similarity of natural categories can lead to the observed enhanced visual activation as reflected by the N1 effect: (1) Perceptual activation to natural categories is greater than to artifactual categories because representations of a larger number of competing exemplars are simultaneously activated by a given picture (see, e.g., Vitkovitch, Humphreys, & Lloyd-Jones, 1993); (2) perceptual information is more strongly weighted in category decisions to natural objects; and (3) in categories with high intracategorical similarity, perceptual features are more informative cues for determining superordinate category membership than in categories with low similarity. Therefore, subjects may have attended more to perceptual properties of natural objects. The latter two interpretations are consistent with results from behavioral studies demonstrating that surface details (e.g., color and texture) facilitate naming and categorization of objects from natural categories more strongly than from artifactual categories (Price & Humphreys, 1989; Tanaka & Presnell, 1999). It should be noted that these three possible interpretations for the perceptual N1 effects are not mutually exclusive and at present it is not possible to distinguish between these alternatives. However, all of them (albeit for different reasons) suggest that natural categories are associated with enhanced perceptual processing.

Late ERP Effects

In the time window between about 300 and 500 msec after target presentation, a broad negative deflection was obtained at fronto-central, centro-parietal, and occipito-temporal recording sites that was identified as an N400 ERP component (Kutas & Hillyard, 1980). As it has been frequently noted, N400 amplitude was larger to semantically incongruent than to congruent targets (for an overview, see Kutas & Van Petten, 1994).

Most relevant to the issue of category-specific semantic memory access, ERPs were differentially modulated by natural and artifactual in both input modalities. In particular, ERPs to natural categories were less negative at occipito-temporal electrodes (with a dominance over the right hemisphere), whereas artifactual categories were less negative mainly at fronto-central electrodes (with a dominance over the left hemisphere). Thus, categorization of natural and artifactual categories was associated with a reduction of N400 amplitude at specific electrode sites. From this finding, it can be concluded that these categories are processed in at least partially different brain regions. Furthermore, the presence and the overall similarity of these category-specific effects for both input modalities suggest that they arise from category-specific differences in semantic processing. For the present argumentation it is not relevant whether the N400 ERP wave proper was differentially modulated by natural and artifactual categories or whether a positive potential that was differentially elicited by these categories overlapped with the N400, thereby reducing its amplitude. Both pos-

sibilities imply that these categories are semantically processed in different brain regions.

Semantic categories also differed in the size of the N400 congruency effect (i.e., a larger N400 to incongruent than to congruent targets, as described above): The congruency effect was consistently larger in artifactual than in natural categories. In order to explore the ERP pattern resulting in a larger congruency effect in artifactual categories, ERPs to natural and artifactual categories were compared separately in the congruent and incongruent conditions. It turned out that similar category-specific ERP differences were obtained as described above, but they were specifically related either to congruent or to incongruent targets: In the *congruent* condition, artifactual categories elicited a less negative potential than natural categories at fronto-central and centro-parietal electrode sites. In the *incongruent* condition, in contrast, natural categories were associated with a less negative potential at occipito-temporal and centro-parietal electrode sites. It is unlikely that these category-specific differences in the N400 congruency effect are simply due to decision-related processes or due to differences in semantic expectancy because they are obtained even when there are not any significant RT differences between categories (as observed in the verbal modality in Experiment 2).

Alternatively, it is proposed that the observed interaction between category and congruency reflects a differential enhancement of category-specific processing in the congruent and incongruent conditions, respectively. As already outlined above, Devlin et al. (1998) have suggested that exemplars of artifactual categories share only a few common features. Therefore, accepting a congruent artifact as member of a superordinate category is associated with relatively high demands in semantic processing. In natural categories, in contrast, it is relatively more demanding to reject incongruent targets because features are highly intercorrelated between categories (Devlin et al., 1998). These assumptions imply that in artifacts, category-specific semantic processing is enhanced with congruent targets, whereas in natural kinds, category-specific processing is enhanced with incongruent targets. The pattern of behavioral results in the present experiments is consistent with this assumption (see the discussion of the behavioral data for a detailed explanation of the interaction between category and congruency).

Although category-specific effects were quite similar across target and category probe modalities, they were not entirely identical. For instance, the interaction between category and congruency at fronto-central electrodes was obtained with a pictorial category probe (Experiment 2), but not with a verbal category probe (Experiment 1). Similarly, in the pictorial target modality, artifactual categories elicited a greater left fronto-central activity than natural categories whether the category was probed verbally (Experiment 1) or pictorially (Experiment 2). In the verbal target modality, a bilateral effect was obtained only when a pictorial probe was used. At present, it is difficult to satisfactorily explain these dif-

ferences in category-specific processing across category- and target modalities. Perhaps category-specific processing is enhanced and/or recruits partially different neural circuits when visual information is provided by the category probe and the target object (see, e.g., Lloyd-Jones & Humphreys, 1997a, for a category-specific RT effect in picture but not in word categorization). Further studies are needed to clarify the functional significance of these modality-specific differences.

If we accept the conclusion that the late category-specific effects indeed reflect differences at a semantic level of representation, the question about the underlying factors determining semantic memory structure can be raised. Is it semantic category per se that determines semantic memory organization directly (see, e.g., Caramazza & Shelton, 1998), or is there a more fundamental distinction underlying category-specific semantic memory organization?

The sensory-functional hypothesis was outlined in the introductory section (Warrington & McCarthy, 1987; Warrington & Shallice, 1984). This hypothesis states that for natural categories, visual semantic knowledge is relatively more important than for artifactual categories, whereas artifactual categories depend more on functional knowledge (see Farah & McClelland, 1991, for a computational model with separated but highly interconnected subsystems of visual and functional knowledge). Similarly, Spitzer (1998) has proposed that semantic knowledge is represented in a map-like fashion in multiple cortical areas (see Pulvermüller, 1999, for a neurobiological approach).

In support of the sensory-functional hypothesis, behavioral studies show that subjects differentially use visual versus functional information when dealing with natural and artifactual categories, respectively (Price & Humphreys, 1989; Tanaka & Presnell, 1999; Tranel, Logan, et al., 1997; Vitkovitch et al., 1993). Furthermore, findings from neuroimaging studies are also compatible with this view (Martin et al., 1996; Thompson-Schill, Aguirre, D'Esposito, & Farah, 1999). Frontal areas activated by artifactual categories are anatomically close to the motor cortices. It is possible that action-related/functional semantic knowledge is represented in the anatomical neighborhood of brain areas involved in motor functions. Likewise, occipital-temporal areas activated by natural categories are anatomically close to the visual cortices. Presumably, they represent visual semantic knowledge. Although the localizational value of ERPs has to be viewed with caution (Nunez, 1981), the topography of the present category-specific ERP effects over fronto-central and occipito-temporal areas is consistent with the anatomical locations observed in neuroimaging studies.

The present ERP study extends earlier work on category-specific processing by showing that category-specific effects arise at two temporally distinct processing stages: at an early perceptual stage (about 160–200 msec) and at a later semantic stage (about 300–500 msec). In the pictorial modality, categories differ in perceptual as well as

in semantic processes, whereas in the verbal modality, category-specific processing is confined to the semantic stage (for a similar distinction between the retrieval of perceptual and semantic features, see Flores d'Arcais, Schreuder, & Glazenborg, 1985). It should be noted that the present early perceptual effects with pictorial stimuli do not reflect higher complexity and lower familiarity of objects from natural relative to artifactual categories, as has been the case in earlier studies (Funnell & Sheridan, 1992; Parkin & Stewart, 1993). It is suggested that they arise because perceptual cues are more informative for determining category membership in natural than in artifactual categories due to their greater perceptual similarity (Lloyd-Jones & Humphreys, 1997a, 1997b; Tranel, Logan, et al., 1997).

Finally, it should be noted that the dichotomy of natural and artifactual categories as well as of functional and visual knowledge clearly is a simplification of the richness of semantic knowledge. Semantic knowledge may be derived not only from the visual, but also from other sensory channels. Likewise, "functional" semantic knowledge may be further subdivided. Furthermore, neuropsychological and neuroimaging studies suggest that artifactual and natural categories are not homogenous and can be further differentiated (e.g., Caramazza & Shelton, 1998; Spitzer et al., 1995). More research is needed to appreciate the varieties of semantic knowledge and their organization in human memory.

Conclusion

The present study shows that perceptual and semantic sources of category-specific effects can be distinguished by the sequence of ERP events, as modulated by natural and artifactual categories presented in different input modalities. At an early perceptual stage (about 160–200 msec after target onset), categories differ only in the pictorial modality. The results provide evidence that perceptual features are more important for category identification in natural than in artifactual categories. However, at a later stage that can be related to semantic processing (about 300–500 msec), category-specific ERP differences were observed in both modalities. The study therefore supports the view that semantic knowledge associated with natural and artifactual categories is represented in multiple subsystems that presumably code different aspects of semantic knowledge. The present work also shows that category-specific effects obtained with pictorial stimuli cannot be unequivocally interpreted as reflecting semantic memory organization unless the perceptual and semantic processes underlying these effects can be clearly dissociated.

REFERENCES

- BAJO, M. T. (1988). Semantic facilitation with pictures and words. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, **14**, 579–589.
- BERTRAND, O., PERRIN, F., & PERNIER, J. A. (1985). A theoretical justification of the average reference in topographic evoked potential studies. *Electroencephalography & Clinical Neurophysiology*, **62**, 462–464.
- CARAMAZZA, A., & SHELTON, J. R. (1998). Domain-specific knowledge systems in the brain: The animate–inanimate distinction. *Journal of Cognitive Neuroscience*, **10**, 1–34.
- CORBEIL, J. C., & ARCHAMBAULT, A. (1994). *The Macmillan visual dictionary: Multilingual edition*. Montreal: Macmillan.
- DAMASIO, H., GRABOWSKI, T. J., TRANEL, D., HICHA, R. D., & DAMASIO, A. R. (1996). A neural basis for lexical retrieval. *Nature*, **380**, 499–505.
- DEHAENE, S. (1995). Electrophysiological evidence for category-specific word processing in the normal human brain. *NeuroReport*, **6**, 2153–2157.
- DE RENZI, E., & LUCCELLI, F. (1994). Are semantic systems separately represented in the brain? The case of living category impairment. *Cortex*, **30**, 3–25.
- DEVLIN, J. T., GONNERMAN, L. M., ANDERSEN, E. S., & SEIDENBERG, M. S. (1998). Category-specific semantic deficits in focal and widespread brain damage: A computational account. *Journal of Cognitive Neuroscience*, **10**, 77–94.
- FAHRAH, M. J., & MCCLELLAND, J. L. (1991). A computational model of semantic memory impairment: Modality specificity and emergent category specificity. *Journal of Experimental Psychology: General*, **120**, 339–357.
- FAHRAH, M. J., McMULLEN, P. A., & MEYER, M. M. (1991). Can recognition of living things be selectively impaired? *Neuropsychologia*, **29**, 185–193.
- FLORES D'ARCAIS, G. B., SCHREUDER, R., & GLAZENBORG, G. (1985). Semantic activation during recognition of referential words. *Psychological Research*, **47**, 39–49.
- FUNNELL, E., & SHERIDAN, J. (1992). Categories of knowledge? Unfamiliar aspects of living and nonliving things. *Cognitive Neuropsychology*, **9**, 135–153.
- HUMPHREYS, G. W., & RIDDOCH, M. J. (1987). On telling your fruit from your vegetable: A consideration of category-specific deficits after brain damage. *Trends in Neurosciences*, **10**, 145–148.
- HUMPHREYS, G. W., RIDDOCH, M. J., & QUINLAN, P. T. (1988). Cascade processes in picture identification. *Cognitive Neuropsychology*, **5**, 67–103.
- JOLICEUR, P., GLUCK, M., & KOSSLYN, S. (1984). Picture and names: Making the connection. *Cognitive Psychology*, **16**, 243–275.
- KIEFER, M., WEISBROD, M., KERN, I., MAIER, S., & SPITZER, M. (1998). Right hemisphere activation during indirect semantic priming: Evidence from event-related potentials. *Brain & Language*, **64**, 377–408.
- KOUNIOS, J., & HOLCOMB, P. J. (1994). Concreteness effects in semantic processing: ERP evidence supporting dual coding theory. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, **20**, 804–823.
- KURBAT, M. A. (1997). Can the recognition of living things really be selectively impaired? *Neuropsychologia*, **35**, 813–827.
- KUTAS, M., & HILLYARD, S. A. (1980). Reading senseless sentences: Brain potentials reflect semantic incongruity. *Science*, **207**, 203–205.
- KUTAS, M., & HILLYARD, S. A. (1983). Event-related potentials to grammatical errors and semantic anomalies. *Memory & Cognition*, **11**, 539–550.
- KUTAS, M., & VAN PETTEN, C. K. (1994). Psycholinguistics electrified. In M. A. Gernsbacher (Ed.), *Handbook of psycholinguistics* (pp. 83–143). New York: Academic Press.
- LOYD-JONES, T. J., & HUMPHREYS, G. W. (1997a). Categorizing chairs and naming pears: Category differences in object processing as a function of task and priming. *Memory & Cognition*, **25**, 606–624.
- LOYD-JONES, T. J., & HUMPHREYS, G. W. (1997b). Perceptual differentiation as a source of category effects in object processing: Evidence from naming and object decision. *Memory & Cognition*, **25**, 18–35.
- MANGUN, G. R., & HILLYARD, S. A. (1991). Modulation of sensory-evoked brain potentials provide evidence for changes in perceptual processing during visual-spatial priming. *Journal of Experimental Psychology: Human Perception & Performance*, **17**, 1057–1074.
- MARTIN, A., WIGGS, C. L., UNGERLEIDER, L. G., & HAXBY, J. V. (1996). Neural correlates of category-specific knowledge. *Nature*, **379**, 649–652.
- NUNEZ, P. L. (1981). *Electrical fields of the brain: The neurophysics of EEG*. New York: Oxford University Press.
- OLDFIELD, R. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, **9**, 97–113.
- PARKIN, A. J., & STEWART, F. (1993). Category-specific impairments?

- No. A critique of Sartori et al. *Quarterly Journal of Experimental Psychology*, **46A**, 505-509.
- POTTER, M. C., & FAULCONER, B. A. (1975). Time to understand pictures and words. *Nature*, **253**, 437-438.
- PRICE, C. J., & HUMPHREYS, G. W. (1989). The effects of surface detail on object categorization and naming. *Quarterly Journal of Experimental Psychology*, **41A**, 797-828.
- PULVERMÜLLER, F. (1999). Words in the brain's language. *Behavioral & Brain Sciences*, **22**, 253-336.
- PULVERMÜLLER, F., PREISL, H., LUTZENBERGER, W., & BIRBAUMER, N. (1996). Brain rhythms of language: Nouns vs. verbs. *European Journal of Neuroscience*, **8**, 937-941.
- RUGG, M. D., & COLES, M. G. H. (Eds.) (1995). *Electrophysiology of mind*. Oxford: Oxford University Press.
- RUOFF, A. (1990). *Häufigkeitswörterbuch gesprochener Sprache* (2nd ed.). Tübingen: Niemeyer.
- SACCHETT, C., & HUMPHREYS, G. W. (1992). Calling a squirrel a squirrel but a canoe a wigwag: A category-specific deficit for artefactual objects and body parts. *Cognitive Neuropsychology*, **9**, 73-86.
- SHERIDAN, J., & HUMPHREYS, G. W. (1993). A verbal-semantic category-specific recognition impairment. *Cognitive Neuropsychology*, **10**, 143-184.
- SNODGRASS, J. G., & VANDERWART, M. (1980). Standardized set of 260 pictures: Norms of name agreement, usage agreement, familiarity and visual complexity. *Journal of Experimental Psychology: Human Learning & Memory*, **6**, 174-215.
- SNYDER, A. Z., ABDULLAEV, Y. G., POSNER, M. I., & RAICHLE, M. E. (1995). Scalp electrical potentials reflect regional blood flow responses during processing of written words. *Proceedings of the National Academy of Sciences*, **92**, 1689-1693.
- SPITZER, M. (1998). *The mind within the net: Models of learning, thinking and acting*. Cambridge, MA: MIT Press.
- SPITZER, M., KWONG, K. K., KENNEDY, W., ROSEN, B. R., & BELLIVEAU, J. W. (1995). Category-specific brain activation in fMRI during picture naming. *NeuroReport*, **6**, 2109-2112.
- TANAKA, J. W., LUU, P., WEISBROD, M., & KIEFER, M. (1999). Tracking the time course of object categorization using event-related potentials. *NeuroReport*, **10**, 829-835.
- TANAKA, J. W., & PRESNELL, L. M. (1999). Color diagnosticity and object recognition. *Perception & Psychophysics*, **61**, 1140-1153.
- THOMPSON-SCHILL, S. L., AGUIRRE, G. K., D'ESPOSITO, M. D., & FARAH, M. J. (1999). A neural basis for category and modality specificity of semantic knowledge. *Neuropsychologia*, **37**, 671-676.
- THORPE, S., FIZE, D., & MARLOT, C. (1996). Speed of processing in the human visual system. *Nature*, **381**, 520-521.
- TRANDEL, D., DAMASIO, H., & DAMASIO, A. R. (1997). A neural basis for the retrieval of conceptual knowledge. *Neuropsychologia*, **35**, 1319-1327.
- TRANDEL, D., LOGAN, C. G., FRANK, R. J., & DAMASIO, A. R. (1997). Explaining category-related effects in the retrieval of conceptual and lexical knowledge for concrete entities: Operationalization and analysis of factors. *Neuropsychologia*, **35**, 1329-1339.
- TUCKER, D. M. (1993). Spatial sampling of head electrical fields: The geodesic sensor net. *Electroencephalography & Clinical Neurophysiology*, **87**, 154-163.
- VITKOVITCH, M., HUMPHREYS, G. W., & LLOYD-JONES, T. J. (1993). On naming a giraffe a zebra: Picture naming errors across different object categories. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, **19**, 243-259.
- WARRINGTON, E. K., & MCCARTHY, R. (1987). Categories of knowledge. *Brain*, **110**, 1273-1296.
- WARRINGTON, E. K., & SHALLICE, T. (1984). Category specific semantic impairments. *Brain*, **107**, 829-854.

NOTE

1. Both the N1 and the N400 ERP components partially overlapped with a positive wave (P1 and LPC, respectively) in some scalp regions. Therefore, they only appear as negative deflections in the waveforms rather than as a negative potential. At these electrodes, a less positive potential in one experimental condition relative to a different condition indexes a greater N1 or N400. However, for clarity reasons, the term "more negative" is always used in this text to indicate a greater N1 or N400.

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