

# How the Camel Lost Its Hump: The Impact of Object Typicality on Event-related Potential Signals in Object Decision

O. Hauk<sup>1</sup>, K. Patterson<sup>1</sup>, A. Woollams<sup>1</sup>, E. Cooper-Pye<sup>1</sup>,  
F. Pulvermüller<sup>1</sup>, and T. T. Rogers<sup>1,2</sup>

## Abstract

■ Using an object decision task, event-related potentials (ERPs), and minimum norm current source estimates, we investigated early spatiotemporal aspects of cortical activation elicited by line drawings that were manipulated on two dimensions: *authenticity* and *typicality*. Authentic objects were those that match real-world experience, whereas nonauthentic objects were “doctored” by deletion or addition of features (e.g., a camel with its hump removed, a hammer with two handles). The main manipulation of interest for both authentic and nonauthentic objects was the degree of typicality in the object’s structure: typical items are composed of parts that have tended to co-occur across many different objects in the perceiver’s experience. The ERP pattern revealed a significant typicality effect at 116 msec after stimulus onset. Both atypical

authentic objects (e.g., a camel with its hump) and atypical nonauthentic objects (e.g., a jackal with a hump) elicited stronger brain activation than did objects with typical structure. A significant effect of authenticity was observed at 480 msec, with stronger activation for the nonauthentic objects. The factors of typicality and authenticity interacted at 160 and 330 msec. The most prominent source of the typicality effect was the bilateral occipitotemporal cortex, whereas the interaction and the authenticity effects were mainly observed in the more anterior bilateral temporal cortex. These findings support the hypothesis that within the first few hundred milliseconds after stimulus presentation onset, visual-form-related perceptual and conceptual processes represent distinct but interacting stages in object recognition. ■

## INTRODUCTION

Object recognition plays an essential role in our interpretation of the environment and forms the basis for many other cognitive processes by which we interact with the world around us. The cognitive and neural processes underlying object recognition still remain, something of a mystery, however. Upon encountering the new neighbor’s dog for the first time, how do we discern that this never-before-seen object is the same “kind of thing” as all the previous dogs of our acquaintance, and furthermore, how are we able to make inferences about its likely behaviors and other nonobvious characteristics? Perhaps the most widely held answer to such questions is the suggestion of Marr and Nishihara (1978) and many others (e.g., Humphreys, Lamote, & Lloyd-Jones, 1995; Biederman, 1987; Jolicoeur, Gluck, & Kosslyn, 1984) that retrieval of semantic information about a visually presented item occurs in distinct stages, including (a) *perception*, that is, the construction of a visuospatial representation of the observed object, (b) *recognition*, or matching of the perceptual representation to a stored

structural description of the class of objects to which the stimulus belongs, and (c) *retrieval* of semantic information about the object. Partly on the basis of double dissociations observed in neuropsychological case studies (see, e.g., Hillis & Caramazza, 1995; Humphreys & Riddoch, 1987; Riddoch & Humphreys, 1987), these three stages are often held to be independent of one another.

Other recent evidence from neuropsychology and functional imaging suggests, however, that visual object recognition and semantic retrieval may be more intertwined than previously suspected (see, e.g., Grill-Spector & Kanwisher, 2005; Rogers, Lambon Ralph, Garrard, et al., 2004; Humphreys & Forde, 2001; Pulvermüller, 2001). For example, Grill-Spector and Kanwisher (2005) reported that subjects categorized pictures of objects as quickly as they detected them, suggesting that these processes occur near simultaneously. Research in primates along with event-related potential (ERP) work in humans has shown that visual stimuli activate a large network of brain areas—including higher order as well as visual areas—almost in parallel within 200 msec after stimulus onset, further questioning strictly serial models of object recognition (e.g., Michel, Seeck, & Murray, 2004; Bullier, 2001).

<sup>1</sup>MRC Cognition and Brain Sciences Unit, Cambridge, UK, <sup>2</sup>University of Wisconsin, Madison

Most striking clinical evidence for an interaction between perceptual and semantic information recently comes from patients suffering from semantic dementia (SD), who have significantly degraded semantic knowledge (whether tested with objects or words), yet have relatively preserved perceptual processing (Patterson et al., 2006; Hodges & Patterson, 1996; Hodges, Patterson, Oxbury, & Funnell, 1992; Snowden, Neary, Mann, Goulding, & Testa, 1992). Notably, their decisions about whether they recognize a stimulus as real appear to be based largely on the familiarity and structural typicality of the input pattern. For example, offered a choice between a picture of an authentic but relatively unfamiliar and visually unusual object (e.g., a real humped camel) and a nonauthentic but more visually typical version of that object (e.g., a camel without its hump), patients with moderate to severe SD prefer the camel without its hump as the real animal (Patterson et al., 2006; Rogers, Lambon Ralph, Hodges, & Patterson, 2004). Precisely the same phenomenon is observed in the patients' word recognition: Offered a choice between a relatively infrequent but authentic written word with atypical orthographic structure (e.g., *yacht* in English) and an nonauthentic pseudoword more typical of the language's spelling patterns (e.g., *yot*), patients with moderate to severe SD are more likely to "recognize" *yot* than *yacht* as the real word (Patterson et al., 2006; Rogers, Lambon Ralph, Hodges, et al., 2004). These findings suggest that recognition of a visual stimulus as authentic depends not only on perceptual/structural analysis but also on interaction with semantic information about the word or object. When the semantic influence is degraded, judgments increasingly reflect *just* the structural influences, so that objects with common combinations of parts (or words with common combinations of letters) are judged to be "real" whether they are or not, especially when the stimulus is not so frequent or familiar as to be overlearned.

To determine the stages of processing at which these factors have their impact, it is necessary to monitor the time course of visual object recognition in humans with millisecond precision. This can only be accomplished with electrophysiological methods such as electro- and magnetoencephalography (EEG and MEG, respectively). The present experiment therefore set out to investigate the influence of structural/perceptual and semantic factors on ERPs in visual object recognition, focusing in particular on whether they have clearly differentiable signatures and on whether there are stages at which they interact. Several previous studies have used EEG or MEG to explore the time course of such influences in visual object processing from different angles, but conclusions from this work have been somewhat mixed. For example, Kiefer (2001) studied ERP responses to pictures of natural kinds and man-made objects while subjects performed superordinate categorizations, and reported that ERPs for the two categories differed sig-

nificantly at 160 msec after picture onset. Because this effect was not elicited by word stimuli, the author attributed the difference to perceptual processing. A later effect around 300–500 msec, which was present for both pictorial and word stimuli, was attributed to conceptual processing. Another study recently found ERP differences for animal and tool pictures in a time window from 200 to 600 msec in a naming task; these results were also interpreted as reflecting differences in semantic rather than perceptual analysis (Sitnikova, West, Kuperberg, & Holcomb, 2006). Such findings are consistent with the standard view that objects first engage perceptual structural descriptions (i.e., in the first 200 msec of processing) and only later engage the semantic system (between 200 and 600 msec).

Somewhat at odds with these conclusions, however, are models of picture naming in which both visual and conceptual information are thought to be retrieved within the first 150 msec (Levelt, Praamstra, Meyer, Helenius, & Salmelin, 1998; Levelt, 1995); these have found partial support in a number of EEG and MEG studies of overt and covert object naming (Hauk, Rockstroh, & Eulitz, 2001; Eulitz, Hauk, & Cohen, 2000; Schmitt, Munte, & Kutas, 2000; Levelt et al., 1998; Salmelin, Hari, Lounasmaa, & Sams, 1994). Also, studies of visual object classification have shown differences in the ERP for conceptually distinct target versus nontarget pictures arising as early as 184 (Johnson & Olshausen, 2005) or 150 msec (VanRullen & Thorpe, 2001) after stimulus onset, suggesting a relatively early engagement of the semantic system. Furthermore, Johnson and Olshausen (2005) argued that this neurophysiological distinction does not reflect object processing itself, but rather postsensory processes such as decision making, which suggests that some perceptual and semantic information must have been extracted even earlier. These and other electrophysiological studies (e.g., Michel et al., 2004) suggest that conceptual systems are engaged quite early in visual object processing.

There are several reasons why previous studies may have had difficulties differentiating perceptual and conceptual processes in visual object processing with ERPs. First, many of the studies reviewed above employed tasks that draw on both vision and language (e.g., naming and categorization), so that the resulting ERP signals may reflect a blend of perceptual, linguistic, and semantic processing. Second, object processing is relatively complex: Compared to word stimuli, for example, there is more interstimulus variability among objects, pictures are composed of a greater array of features than words, and so on. Consequently, one might expect a somewhat more extended time course for object processing relative to words, and if processing is cascaded rather than strictly staged (i.e., early processes need not be fully completed before they begin to send information to later processes), the extended time course may make it especially difficult to discriminate "perceptual" and "conceptual" processes. Third,

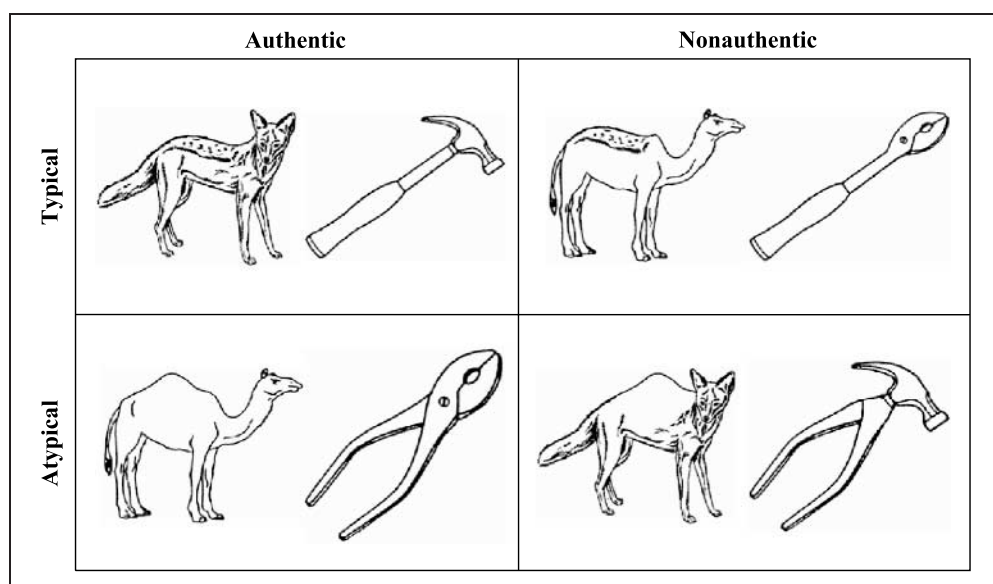
because semantically related items also tend to share visual attributes, it is difficult to deconfound semantic and visual processing. Where category effects are observed, for instance, it is often unclear whether they arise because items from different categories have different “meanings” or because they have different visual characteristics. In particular, no previous study has investigated the neurophysiological correlates of visual structural typicality.

The present study aims to address these challenges by investigating neurophysiological processes in a task that involves viewing black and white line drawings and judging whether they depict real objects (i.e., object decision). This task has been shown to be sensitive (a) in patients with SD, to the degree of semantic impairment (Hovius, Kellenbach, Graham, Hodges, & Patterson, 2003; Rogers, Lambon Ralph, Hodges, & Patterson, 2003) and (b) in neurologically normal participants, to differences in the degree to which the judgements required discrimination of visual and semantic features (Lloyd-Jones & Luckhurst, 2002a, 2002b; Gerlach, 2001; Gerlach, Law, Gade, & Paulson, 1999). Half of the line drawings in our set depicted *authentic* objects that exist in the real world, and these were further classified as *atypical* if they included a prominent and uncommon structural feature (for instance, the camel, which has a hump on its back), or lacked a prominent and common one (e.g., the seal, which lacks the four legs common to most mammals), and *typical* otherwise (for instance, the jackal, which has no very salient distinguishing structural features; see Figure 1). The remaining line drawings depicted *nonauthentic* objects, created by deleting features from or adding features to

the authentic objects. This doctoring turned half of the nonauthentic objects into relatively typical things (e.g., a camel with its hump removed, making it more structurally similar to other four-legged creatures than the real camel) and the remaining half into atypical things (a jackal with a hump added, making it less structurally similar to other four-legged creatures than the real jackal). Thus, the stimuli orthogonally varied *authenticity* and *structural typicality*. Participants viewed the items in random order and, for each, indicated by button-press whether they believed it to be a real (i.e., authentic) object.

The object-decision task addresses the challenges listed above in the following ways. First, it makes minimal demands on linguistic processing—the stimuli need not be named in order to be judged as real—and so minimizes the problem of potential cross-talk from language-processing systems. Second, because the response is a simple yes/no button press, the ERP time course should be as compact as it is possible to be in a visual object-processing task. Third and most important, the task allows us to discriminate true recognition processes from perceptual processes that are sensitive to visual structure. Although all visual stimuli must engage visual/structural processes, only authentic items (be they structurally typical or atypical) ought to be recognized—so a main effect of authenticity should indicate the processes that support recognition. In contrast, structurally typical items, because they are composed of parts that frequently co-occur, should be processed more efficiently in the visual/structural system than structurally atypical items, regardless of whether they are authentic; hence, a main effect of structural typicality should

**Figure 1.** Examples of line drawings employed in our experiment in the four conditions. A jackal is a typical animal, as it has a flat back, whereas a camel is an atypical animal, as it has a hump. Similarly, a hammer is a typical tool, as it has a single handle, whereas pliers are an atypical tool, as they have two handles. By giving the camel a flat back, it becomes a typical nonauthentic object, and by giving the jackal a hump, it becomes an atypical nonauthentic object. Similarly, by giving the pliers a single handle, it becomes a typical nonauthentic object, and by giving the hammer two handles, it becomes an atypical nonauthentic object. Descriptions of the full set of line drawings used are provided in the Appendix.



indicate perceptual processes sensitive to visual structure. Interactions between perceptual and recognition processes should, accordingly, be marked by the interaction of authenticity and structural typicality.

The study is analogous to a previous investigation in which we used ERPs to provide neurophysiological evidence for separate but interacting structural and semantic processes in visual word recognition (Hauk et al., 2006). In that study, we orthogonally varied the typicality and lexicality of visually presented letter strings in a yes/no lexical decision task with healthy participants. On various trials, participants made lexical decisions to authentic words with an orthographic structure typical for English (e.g., *cart*), authentic but atypical words (e.g., *yacht*), nonauthentic letter strings with typical structure (e.g., *yart*), or nonauthentic atypical letter strings (e.g., *cacht*). We observed a main effect of typicality (more activation to atypical letter strings, independent of their lexical status) around 100 msec after word onset; a main effect of lexicality (more activation to pseudowords than words irrespective of their typicality) around 200 msec; and an interaction of these two factors occurring in between, at around 160 msec. We interpreted this as evidence for distinct structural and semantic lexical processes that interact in a cascaded processing sequence in visual word recognition.

In the present study, we recorded multichannel ERP responses while participants performed an object recognition task in order to study the topography and time course of visual object recognition. Meticulous matching was performed to control for physical stimulus features. The stimulus construction procedure minimized the possibility of physical confounds, in that, during the doctoring, each object feature removed from one picture was incorporated in the control category (see Figure 1). Furthermore, we matched our stimulus categories for luminance and visual complexity as revealed by objective measures. In addition to traditional ERP analysis, we applied distributed source estimation analysis, which relies on minimal modeling assumptions, with the goal of determining the brain correlates of typicality and authenticity processing in object recognition.

## METHODS

### Subjects

Fifteen monolingual, English-speaking right-handed subjects (8 women, 7 men; mean age, 23.9 years;  $SD = 6.4$ ) entered the analysis, after data from five subjects were discarded due to high noise levels. No subjects reported a history of neurological illness or drug abuse, and all had normal or corrected-to-normal vision. Handedness as determined by a reduced version of the Oldfield inventory, consisting of 10 questions about the preferred hand in specific actions, revealed a mean laterality quotient of 87.1 ( $SD = 15.3$ ) (Oldfield, 1971).

Informed consent was obtained from all subjects and they were paid for their participation. This study was approved by the Cambridge Psychology Research Ethics Committee.

### Stimuli

The pictures of authentic and nonauthentic items were based on those used in a previous study (Rogers, Lambon Ralph, Hodges, et al., 2004). The original study used a two-alternative forced-choice object decision paradigm: Subjects were confronted on each trial with line drawings of a real object and of a nonreal “chimeric” version of the same object. Their task was to decide which of these line drawings depicted a real object. The crucial manipulation in the Rogers, Lambon Ralph, Hodges, et al. (2004) study was that in some pairs the chimera had more typical features than the real object (e.g., a chimerical elephant with the small ears that are typical of mammals, even big ones, vs. a real elephant with its correct but atypical large ears), whereas in other pairs the real object had more typical features than the chimera (e.g., a monkey with typical small ears versus a chimerical monkey with atypical large ears). Stimuli of this sort have already been successfully applied in previous behavioral and neuroimaging studies (Kellenbach, Hovius, & Patterson, 2005; Hovius et al., 2003). It should be noted that there is no precise and quantifiable definition of “typicality” in this context. We view typicality as the degree to which the features of an object can be expected to occur together. In the comparable case of the typicality of words (see Hauk et al., 2006), an operational definition and approximation of the typicality concept can be given by referring to the frequency of letter bigrams.

In the present experiment, we used a yes/no response on single-object stimulus items, as reaction times (RTs) and neurophysiological responses to individual items were to be investigated. As shown in Figure 1, to create a typical nonauthentic item, we took an atypical authentic item and replaced its idiosyncratic feature with one from a typical authentic item (e.g., replacing the hump of a camel with the back of a jackal, or the two handles of a pair of pliers with the single handle of a hammer). To create an atypical nonauthentic item, we applied the reverse transformation, in that we took a typical authentic item and replaced one of its features with an idiosyncratic one from an atypical authentic item (e.g., replacing the back of a jackal with the hump of a camel, or the single handle of a hammer with the two handles of a pair of pliers). The stimulus items from Rogers, Lambon Ralph, Hodges, et al. (2004) were supplemented with an additional 30 items per condition for use in a preliminary rating study involving 12 participants. We then eliminated 10 items per condition in order to match between the typical and atypical authentic objects in terms of rated familiarity. A



description of the full list of the 200 line drawings used is provided in the Appendix, including familiarity ratings for all items.

The procedure for creating the stimuli ensured that the authentic and nonauthentic objects could not differ markedly with respect to simple visual attributes (such as luminance or visual complexity), because they consisted of the same components in different combinations. However, differences might still occur between typical and atypical items. We therefore tested for differences in luminance by counting the number of black pixels in each image, and a two-by-two analysis of variance (ANOVA) with the factors Authenticity and Typicality conducted on these values revealed no significant differences among categories (all  $F_s < 1.0$ ). In order to obtain measures for visual complexity, we compressed our images (originally in Windows bitmap format) to jpg, tif, and zip format using Matlab software (Version 6.5; The MathWorks Inc., Natick, MA). This compression aims at removing redundant information from the images, therefore providing an indirect measure of the visual complexity of the images. Analysis of these values also did not indicate any significant differences between categories (all  $F_s < 1.0$ ). We also determined noun lemma and word form frequencies for the names of authentic objects as listed in the appendix from the Celex database. Two-tailed  $t$  tests did not reveal a statistically significant difference between typical and atypical authentic items for these parameters.

## Procedure

Subjects performed a yes/no object decision task. They were instructed to respond to real objects and nonreal objects by pressing a button with their left index finger or left middle finger, respectively. A short practice run preceded the experiment proper to ensure that subjects were comfortable with the task. The stimuli of the practice run were not repeated during the following experiment. Black line drawings were presented on a very light gray background on a computer screen approximately 1.5 m in front of the subject, with the size of each stimulus not exceeding a visual angle of  $4^\circ$ .

Each stimulus was presented in the center of the screen for at least 500 msec, and then remained on the screen until a button was pressed or a time-out of 3000 msec was reached. Mean interstimulus interval (ISI) was 3500 msec. The ISI was jittered by an exponential random function with mean 500 msec, and a maximum jitter of 1500 msec. To minimize eye movements, a fixation cross was shown in the center of the screen when no experimental stimulus was present. Each subject was presented with a different random sequence of the same stimuli. Breaks occurred after every 50 stimuli, in which subjects could decide by button press when they wanted to continue the experiment. Stimulus delivery and response collection was controlled

by the Experimental Run Time System software (ERTS, BeriSoft Cooperation, Frankfurt, Germany).

## Data Recording

The electroencephalogram (EEG) was measured in an electrically and acoustically shielded EEG booth at the MRC Cognition and Brain Sciences Unit in Cambridge, UK. Data were recorded from 64 Ag/AgCl electrodes mounted on an electrode cap (EasyCap, Falk Minow Services, Herrsching-Breitbrunn, Germany) using SynAmps amplifiers (NeuroScan Labs, Sterling, VA), arranged according to the extended 10/20 system. Data were acquired with a sampling rate of 500 Hz. Recording reference for the EEG channels was Cz. The electrooculogram (EOG) was recorded bipolarly through electrodes placed above and below the left eye (vertical) and at the outer canthi (horizontal).

## Preprocessing of ERP Data

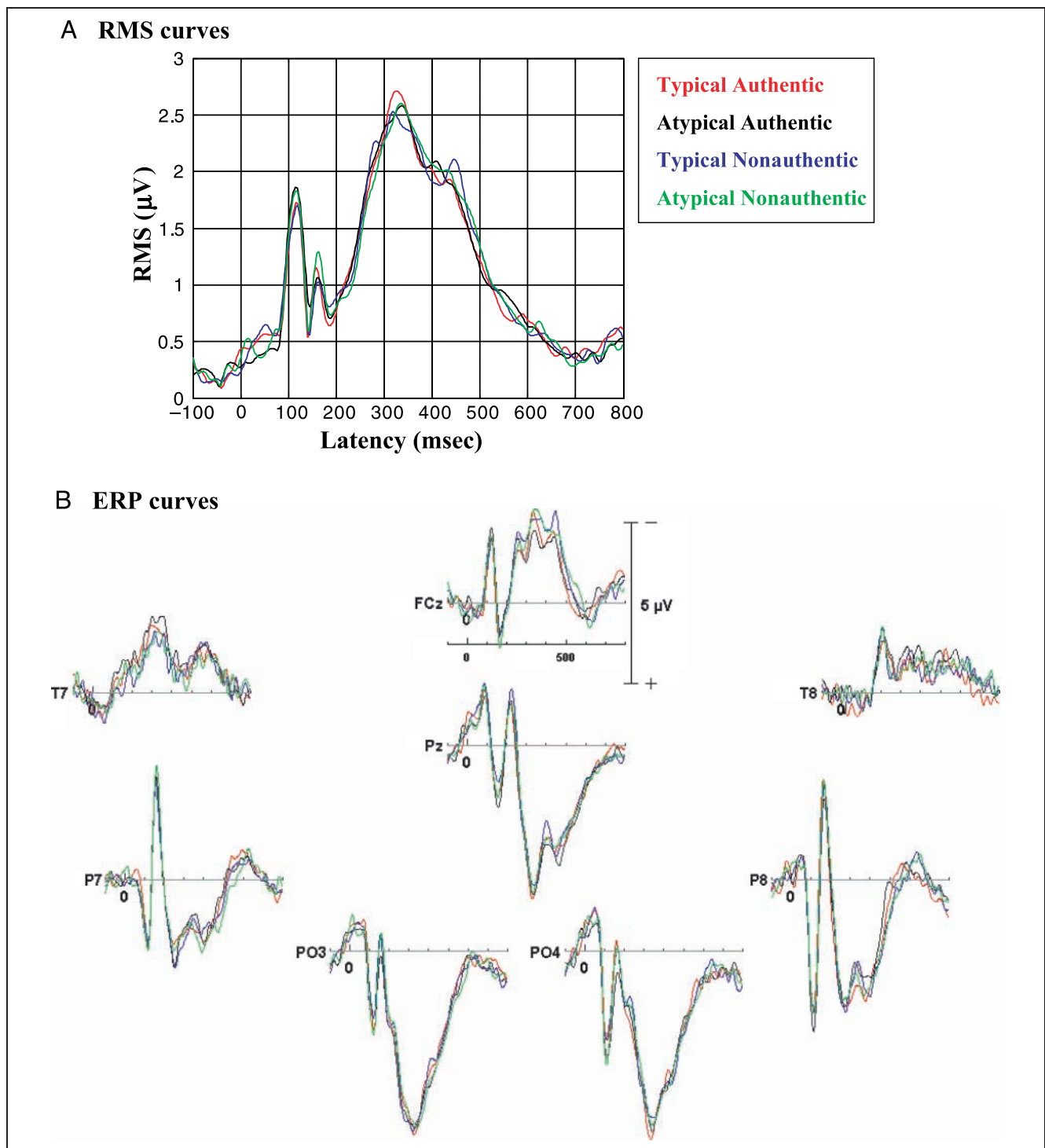
The continuously recorded data were band-pass filtered at 1–20 Hz and transformed to average reference. Epochs of 900-msec duration, including a 100-msec baseline interval, were averaged for each stimulus category. Epochs with peak-to-peak potential differences larger than 100  $\mu\text{V}$  in at least one EEG or EOG channel were rejected. For each channel, the mean amplitude of a 100-msec prestimulus interval was subtracted at all time points. Epochs in which subjects made incorrect responses were excluded from both behavioral and ERP analyses.

## Behavioral Analysis

Reaction times were recorded with respect to the onset of the stimuli. Responses occurring more than 3000 msec after stimulus onset were considered incorrect. ANOVA analyses on RTs and error rates of correct responses were performed by items as well as by subjects.

## Statistical ERP Analysis

Latencies for the analysis of ERP responses were chosen from peaks in the root-mean-square (RMS) curve for the average of the four conditions presented in Figure 2. We attempted to run the same statistical analysis on all of these latency ranges, focusing on electrodes exhibiting peaks in the topographies at the corresponding latencies. The most prominent peaks in the voltage distributions occurred at electrodes P8 (116 msec), P7/P8 (160 msec), PO3/PO4 (330 msec), and Pz (480 msec). In order to cover temporal and more frontal electrode sites as well, we added electrodes T7/T8 and FCz to



**Figure 2.** Illustration of the time course of grand-mean ERP data. (A) RMS curves for individual conditions. (B) Voltage curves for selected electrodes that were used in the statistical analysis for individual conditions (color coding as in A). Main effects of Typicality and Authenticity occurred at 116 and 480 msec, respectively. A Typicality  $\times$  Authenticity interaction was present at 160 and 330 msec.

the analysis. Thus, topographical analysis was performed on eight symmetrical and central electrodes (PO3/PO4, P7/P8, T7/T8, Pz, FCz), yielding an eight-level factor Topography, which was combined with the factors Authenticity (two levels) and Typicality (two levels). Where appropriate, significance levels of interactions involving

the factor Topography will be reported for adjusted degrees of freedom according to Greenhouse–Geisser (Greenhouse & Geisser, 1959). In addition to this restricted analysis, we will also present distributions of *p* values together with the corresponding difference topographies. This provides more complete information

about the distribution of effects, for example about their spatial specificity. The EOG was analyzed statistically for the latencies of interest to rule out eye movements as a possible confound of our ERP effects.

### Source Estimation

Estimating the sources inside the brain generating a given potential distribution at the scalp surface—the so-called inverse problem—does not have a unique solution. The Moore–Penrose pseudoinverse or *minimum norm solution* has been suggested as a reasonable approach: Among the possible source constellations that can explain a given surface topography, this method prefers the least costly solution, the most parsimonious one in terms of the sum of squares of the generators' strengths. Any generator distribution that explains the recorded data is the sum of this minimum norm solution and another source distribution that by itself does not produce any measurable signal at any electrode (Hauk, 2004; Hämäläinen & Ilmoniemi, 1994). The latter type of “silent” source is avoided by this method. It can therefore be considered as relying on a minimum of modeling assumptions, and optimally exploiting the information provided by the recorded data alone in the absence of further *a priori* information.

Our implementation followed the procedure of Hauk (2004), which yields a blurred two-dimensional projection of the true source distribution within the brain. We applied this method to our grand mean data for different conditions, and computed differences between source maps obtained in different conditions in case significant main effects or interactions supported such differences. To assess the reliability of the differences, we used a procedure similar to that of Dale and Sereno (1993); that is, the estimated source strengths were thresholded according to their signal-to-noise ratio (SNR). The SNR was computed at each dipole location by dividing the source strength of each dipole by its standard deviation of the source strengths within the baseline interval. Activation was displayed as nonzero when the SNR exceeded a value of 3.

The limitations of ERP source estimation raise the question of how to associate spots of activation with corresponding brain areas. Because our source estimates were obtained in a realistic head model derived from the standard brain of the Montreal Neurological Institute (MNI), we computed Talairach coordinates for prominent spots of activation (see [www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml](http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml)) and determined the nearest area of gray matter from the Talairach Daemon Database (Version 1.1; Research Imaging Center, University of Texas Health Science Center, San Antonio, TX). We will not report the results at the level of Brodmann areas (BA), but rather refer to anatomical landmarks, for example, gyri and sulci (such as “middle temporal gyrus” rather than BA 21).

## RESULTS

### Behavioral Data

Mean correct RTs and overall error rates are displayed in Table 1. These data were analyzed by ANOVAs including the within-subjects ( $F_s$ ) and between-items ( $F_i$ ) factors of Authenticity (two levels) and Typicality (two levels). The results revealed a reliable main effect of Typicality in RT,  $F_s(1,14) = 25.19, p < .0005$ ;  $F_i(1,196) = 3.88, p = .050$ , but not in accuracy,  $F_s(1,14) = 1.66, p = .218$ ;  $F_i(1,196) < 1$ . The main effect of Authenticity was significant only by items in RT,  $F_s(1,14) = 1.54, p = .235$ ;  $F_i(1,196) = 8.34, p = .004$ , and was not reliable in accuracy ( $F_s$  and  $F_i$  both  $< 1$ ). The interaction between Typicality and Authenticity was not reliable for RT or accuracy, either by subjects or items (all  $F_s < 1$ ). These data indicate that subjects were able to respond more rapidly to atypical than typical objects, irrespective of whether those objects were real or not.

### Event-related Potentials

Distinct peaks in the RMS curve of the average across all conditions occurred at latencies 116, 160, and 330 msec, with a further not very distinct peak at 438 msec (see Figure 2). The difference curves for the authentic and nonauthentic categories produced their largest RMS peak at 480 msec, and we therefore selected this as the latest latency for further analysis. As can be seen in Figure 2A and B, the RMS and ERP curves for individual conditions demonstrate that their time courses and baseline activities are similar.

A summary of significant effects is presented in Table 2. In brief, a main effect of Typicality at 116 msec was followed by a significant interaction between Authenticity and Typicality at 160 msec and a marginally significant one at 330 msec. Finally, there was a main effect of Authenticity at 480 msec.

For the selection of all eight electrodes, we obtained a marginally significant interaction between Typicality and Topography at 116 msec,  $F(7,98) = 2.29, p = .073, \epsilon = 0.55$ . The difference ERP for atypical and typical items peaked at electrode PO4. An ANOVA performed on peak electrodes PO3 and PO4 revealed a significant

**Table 1.** Summary of Behavioral Results of the Object Decision Task (Average RTs and Error Rates) as a Function of Authenticity and Typicality

	RT (msec)	Error Rate (%)
Typical authentic	1136	13.2
Atypical authentic	1071	11.2
Typical nonauthentic	1180	14.8
Atypical nonauthentic	1133	14.0

**Table 2.** Summary of ANOVA Results at Peak Latencies

	116 msec	160 msec	330 msec	480 msec
Authenticity	–	–	–	× Topography: $p < .02$ Main effect: $p < .02$
Typicality	× Topography: $p < .08$ Main effect: $p < .02$	× Topography: $p < .07$	–	–
Authenticity × Typicality	–	$p < .02$	$p = .07$	–

Effects of Authenticity and Typicality (upper two rows of table) are reported either as an interaction with the additional factor Topography (eight selected electrodes), or as main effects on a subset of peak electrodes (PO3 and PO4 at 116 msec, FCz at 480 msec). The interaction Authenticity × Typicality × Topography did not reach significance in any comparison and was therefore not included in this table. Empty cells refer to nonsignificant effects.

main effect of Typicality,  $F(1,14) = 7.75$ ,  $p < .02$ , with atypical items producing larger positive amplitudes than typical items. The corresponding ERP topography and  $p$  value distribution is presented in Figure 3A, which confirms stronger positive amplitudes for atypical items at right occipitoparietal electrode sites. There was no significant effect of Authenticity at this early latency.

A marginally significant interaction between Typicality and Topography was also present at 160 msec,  $F(7,98) = 2.45$ ,  $p = .068$ ,  $\epsilon = 0.53$ . Again, the maximum difference occurred at electrode PO4 with more positive amplitudes for atypical items. However, the analysis restricted to PO3 and PO4 did not reveal significant effects of Typicality. Critically, the interaction between Authenticity and Typicality was significant at this latency in the analysis of data from all eight electrodes,  $F(1,14) = 7.42$ ,  $p < .02$ . Post hoc tests revealed a significant effect of authenticity for atypical items,  $F(1,14) = 5.78$ ,  $p < .05$ , but no such effect for typical items.

The interaction between Authenticity and Typicality approached significance over all eight electrodes again at 330 msec,  $F(1,14) = 3.78$ ,  $p = .072$ , as did the main effect Typicality,  $F(1,14) = 4.02$ ,  $p = .065$ . Post hoc  $t$  tests revealed that the only significant simple effect was a typicality effect for authentic items,  $F(1,14) = 6.36$ ,  $p < .05$ . The average amplitudes across all eight electrodes for the interactions at 160 and 330 msec are displayed in Figure 4B.

An interaction between Authenticity and Topography was apparent at 480 msec,  $F(7,98) = 4.33$ ,  $p < .05$ ,  $\epsilon = 0.39$ . This effect was maximal and statistically reliable at electrode FCz,  $F(1,14) = 8.96$ ,  $p < .05$ , where non-authentic items were more negative in amplitude than authentic items. The voltage and  $p$  value distributions for this effect are displayed in Figure 3B.

Figure 5A presents minimum norm source estimates for the main effect of Typicality at 116 msec. Atypical items produced maximum activation compared to their typical counterparts in the right posterior superior temporal gyrus, and a weaker peak of activity in the homotopic area in the left hemisphere. Maximum activation for typical items occurred in the right middle frontal

gyrus. Figure 5B presents minimum norm source estimates for the main effect of Authenticity at 480 msec, which was characterized by stronger activation for non-authentic items compared with authentic ones in the left and right inferior temporal lobe and right inferior frontal gyrus.

Figure 6 shows source distributions estimated at 160 and 330 msec. Because at these latencies no reliable interactions with Topography were found, source estimates were computed for the ERP averaged across all four conditions. At both latencies, temporooccipital current sources emerged bilaterally. At 160 msec, activation peaks were present in both middle temporal gyri. At 330 msec, the right activation peak appeared once again in the middle temporal gyrus, whereas the activation peak in the left hemisphere was in the middle occipital gyrus.

Finally, we analyzed both vertical and horizontal EOG signals separately using an ANOVA including the factors Authenticity and Typicality, at the latencies for which we reported effects in the ERP above. None of these tests yielded significant results, excluding eye movements as a possible confound for our ERP effects.

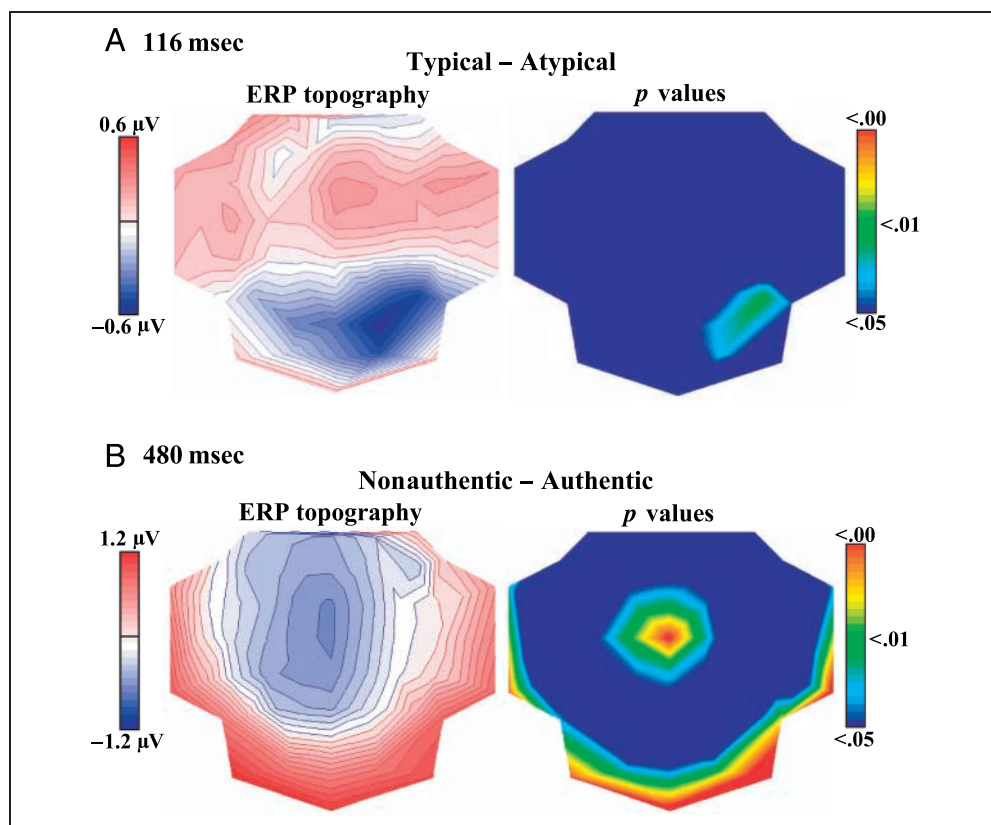
## DISCUSSION

### Behavioral Effects

To our knowledge, this is the first study to manipulate structural typicality in an object-decision task with neurologically normal participants. The behavioral data are therefore of some interest in their own right, and revealed two findings of note. First, whereas past studies of object decision (e.g., Kellenbach et al., 2005) have found correct “no” decisions to be significantly slower than correct “yes” decisions, the trend toward slower no than yes decisions was not statistically reliable in the present experiment. The result may reflect the careful matching of targets and distractors for structurally typicality. Common tests of object decision have not typically controlled for this factor. For instance, in an analysis of the Birmingham Object Recognition Battery (Riddoch & Humphreys, 1993), Rogers et al. (2003)



**Figure 3.** Topographical maps for the effects involving either the factor Typicality or Authenticity at latencies 116 and 480 msec. Difference topographies (typical minus atypical and nonauthentic minus authentic, respectively) are shown on the left. Statistical  $p$  maps for the corresponding contrasts (paired two-tailed tests) are presented on the right. The electrode array was unfolded onto one plane for better visualization.

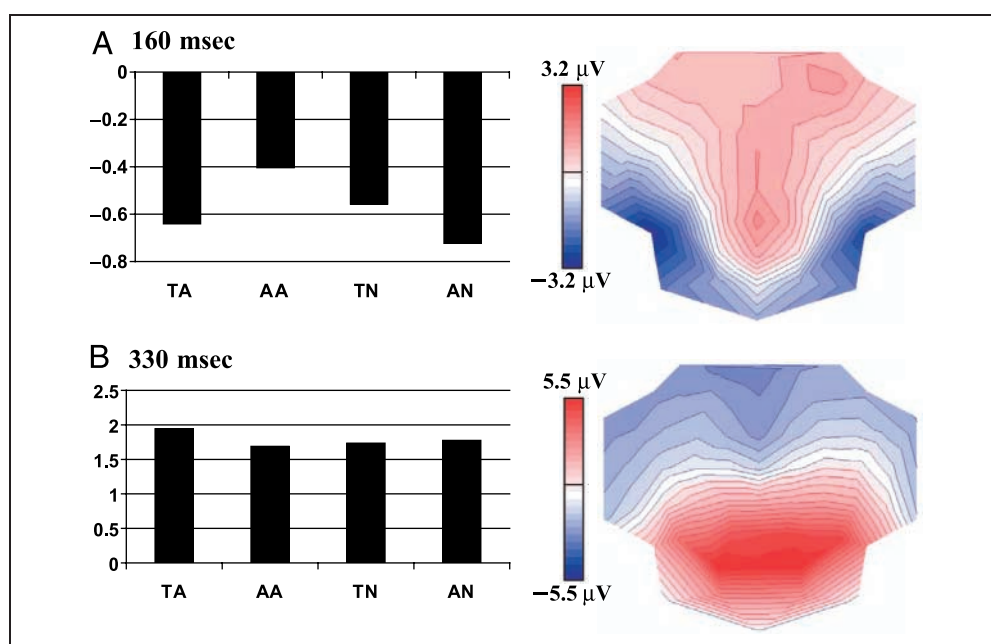


found that the majority of chimeric distractors (53 of 64 items) were structurally unusual in some respect, whereas the real-object targets included a more varied mix of structurally typical and unusual items. Such a discrepancy could promote overall faster responding to targets because they are typical as well as authentic. In the current study, structural typicality is completely de-

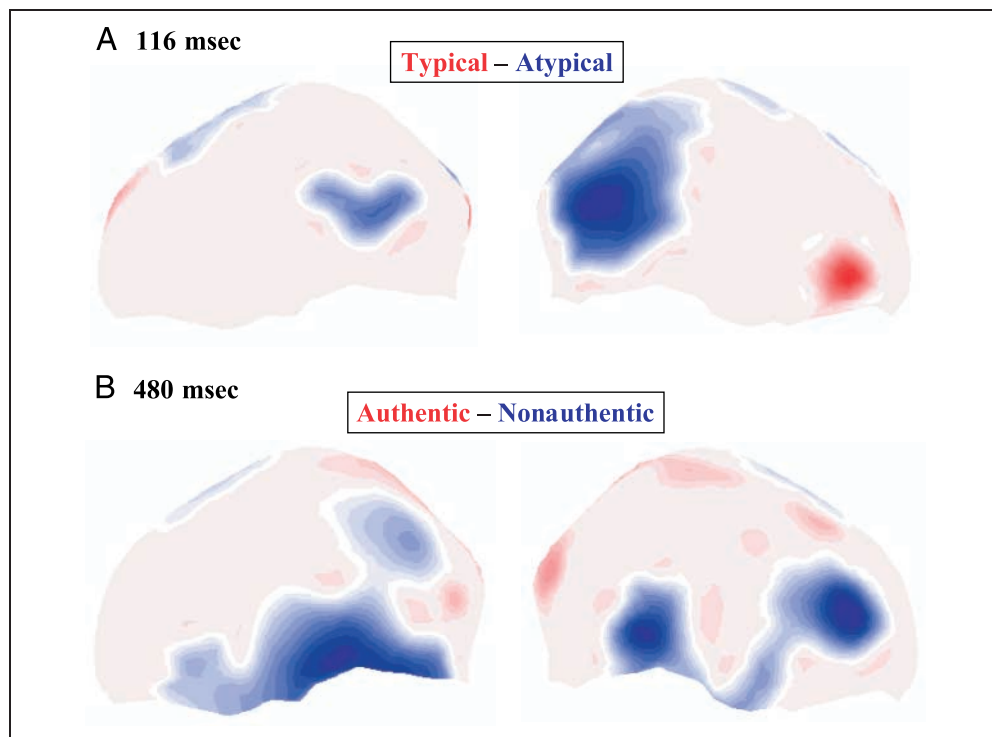
confounded from authenticity, such that participants cannot base their decision upon overall structural “goodness” for any stimuli.

Second and perhaps more striking was the reliable main effect of typicality, reflecting significantly *faster* responses for atypical than typical items, irrespective of whether the decision made was no or yes. One in-

**Figure 4.** Summary of the effects involving both factors Typicality and Authenticity at 160 (A) and 330 msec (B). The bar graphs present average voltages across electrodes used in the statistical analysis for each individual condition. The topographical maps show the voltage distribution at the corresponding latency for the average across conditions. Because the interaction did not involve the factor Topography, no topographies for individual contrasts are presented. TA = typical authentic; AA = atypical authentic; TN = typical nonauthentic; AN = atypical nonauthentic.



**Figure 5.** Difference source distributions for the effects involving either the factor Typicality or Authenticity at latencies 116 (A) and 480 msec (B). Source estimates are displayed for the left and the right hemisphere at the left and right of the image, respectively. Source strengths are only displayed as nonzero at locations where their SNRs were higher than 3. Red and blue colors distinguish the direction of effects according to labels within each figure.



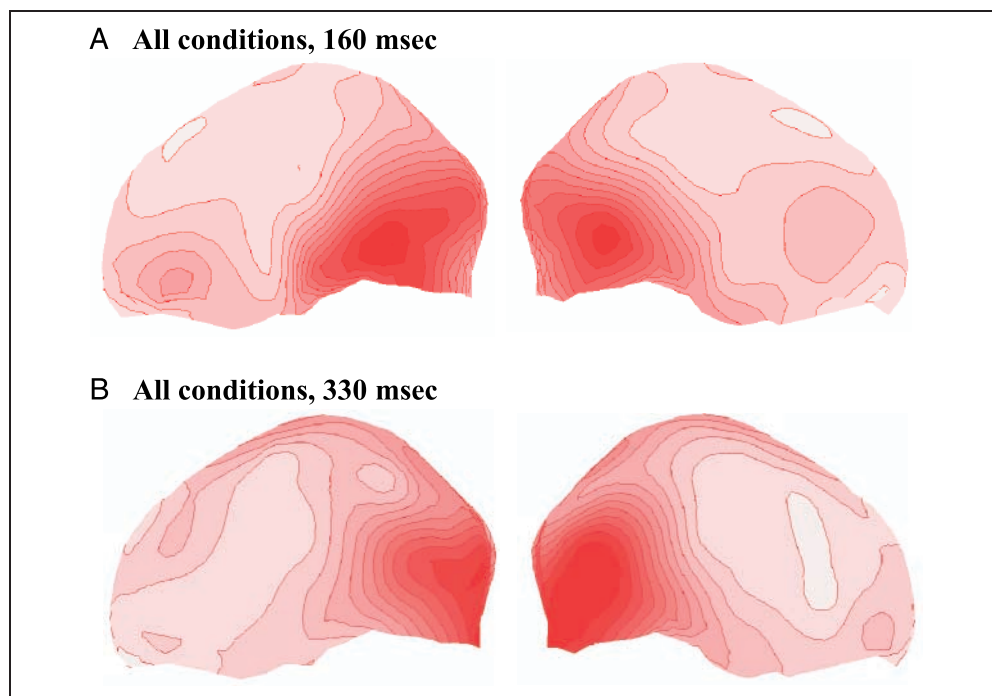
interpretation of the effect is that, for atypical items, attention is captured by the atypical feature (e.g., large ears), which in turn generates a candidate set of compatible objects (e.g., elephants, rabbits, etc.) to be matched against the rest of the object image. As, by definition, fewer objects in the real world possess atypical than typical features, the candidate set will be smaller for atypical than typical items, allowing a decision to

be made more rapidly for atypical items (Humphreys et al., 1995).

### Spatiotemporal Pattern of the ERP

Two main effects were observed within the first 500 msec poststimulus onset: an early effect (116 msec) of structural typicality, uninfluenced by authenticity and with

**Figure 6.** Source distributions for the average ERP across conditions at latencies 160 and 330 msec. Conventions as in Figure 5. Because no differences were computed in this case, the intensity distribution has entirely positive values.



atypical items producing larger amplitudes than typical items; and a later effect (480 msec) of authenticity, uninfluenced by typicality and with nonauthentic items producing larger amplitudes than authentic items. Between these main effects were two interactions: the first showing significant differences between authentic and nonauthentic items for atypical but not typical items, and the second, only marginally significant, showing differences between typical and atypical items for authentic items, but not nonauthentic items.

### **Main Effect of Typicality**

The typicality effect at 116 msec is consistent with the view that early visual processing is sensitive to the correlational structure of the visual components of the stimulus, whether or not it is a real object. That is, items composed of parts that have tended to occur together across many different objects in the perceiver's experience (i.e., structurally typical items) may be processed more efficiently, because the presence of each individual component tends to support/predict the presence of all the other components. Items with prominent visual features that are not well predicted by other components of the object—atypical items—will challenge visual processes that are sensitive to such correlational structure, reflected by larger amplitudes in the ERP. The view that the typicality effect arises predominantly from visual processing is further supported by the source estimates for the effect, which showed a strong activation in superior occipito-temporal regions on the right, and weaker activation in homologous regions in the left. The more anterior and inferior temporal lobe regions thought critical to semantic processing (e.g., Price, 2000) were not strongly activated at this point in time. Note that the effect is unlikely to reflect differences in low-level visual characteristics because we took great care to match our typical and atypical (as well as authentic and nonauthentic) stimuli with respect to luminance and visual complexity.

The result is also consistent with previous work suggesting that visual processing sensitive to long-term experience begins around 125 msec (Schendan, Ganis, & Kutas, 1998). For instance, several studies of visual processing have reported differential modulation of electrophysiological responses at around 100 msec in a variety of contrasts: for words versus pictures (Rossion, Joyce, Cottrell, & Tarr, 2003), for faces versus control images (Halgren, Raij, Marinkovic, Jousmaki, & Hari, 2000), and for pictures of animals versus vehicles (VanRullen & Thorpe, 2001). Our data suggest that such results may not reflect categorization or recognition in the sense of matching an observed stimulus to a stored representation. Instead they may arise because the stimuli in the different contrast conditions differ in their structural typicality—in the extent to which their visual features cohere in past experience and so pro-

mote rapid processing at this early stage. Under this view, the early visual process is still performing a form of categorization—it is distinguishing input patterns that seem likely to represent a known object (because they consist of oft-encountered combinations of features) from those that are unlikely to reflect familiar objects.

### **Main Effect of Authenticity**

The main effect of authenticity at 480 msec did not interact with structural typicality and so appears to reflect a true “recognition” signal, differentiating real/familiar items from nonreal/unfamiliar items. The signal was characterized by a fronto-central negativity in the ERP, a pattern that has previously been related to semantic processing of words and pictures (Kiefer, 2001; Kutas & Federmeier, 2000; Holcomb & McPherson, 1994; Barrett & Rugg, 1990). The current finding is therefore consistent with the view that differentiation of authentic from nonauthentic items in this task depends upon semantic processes.

This interpretation is further supported by the source estimates, which revealed activation in bilateral inferior temporal lobes on both sides as far forward as the temporal pole, thus conforming to some current theories about the neural basis of visual–semantic processing. The direction of the effect—more activation for non-objects than for objects—indicates that authentic (i.e., recognizable) objects were processed more efficiently than nonauthentic objects in this system. Note that our nonauthentic items, which can be described as chimeras, differ from the “nonobjects” used in some previous studies (e.g., Gerlach et al., 1999; Schendan et al., 1998; Holcomb & McPherson, 1994) in that all their components exist in the real world, and their combinations are not completely implausible, but merely contradict experience. It seems likely, therefore, that such nonauthentic items will engage the semantic system in this task (because their parts are recognizable), but inefficiently (because the conjunction of parts does not correspond to a particular recognizable concept).

### **Interactions between Typicality and Authenticity**

Between the early main effect of typicality and the later main effect of authenticity, we observed two interactions between these factors, neither of which interacted with topography. The earliest, occurring around 160 msec poststimulus, indicated a significant difference between authentic and nonauthentic items for atypical but not typical stimuli. The main estimated sources at 160 msec occurred in the bilateral middle temporal gyrus. The later interaction, which was only marginally significant, was observed at 330 msec and reflected a significant typicality effect for authentic but not nonauthentic

items. The source estimates for this effect revealed a right-hemisphere peak in the middle temporal gyrus and a left-hemisphere peak in the middle occipital gyrus. Because this is the first ERP study of object recognition to manipulate these factors, we had no grounds for precise predictions about the form that their interaction might take. We merely had, on the basis of our previous investigation of typicality and authenticity in lexical decision (Hauk et al., 2006), predicted (a) that these factors would once again interact in the ERP signals associated with object decision; (b) that they might well do so in the time range between an early main effect of typicality and a later main effect of authenticity; and (c) that the source estimates associated with the interaction(s) would be temporal or occipitotemporal, regions that have been shown to be involved in both higher order visual and semantic processing (Kellenbach et al., 2005; Grill-Spector, 2003; Price, 2000). The results conform to all of these expectations.

### Conclusions from ERP Data

In summary, our data are consistent with the view that visual object recognition is supported by two separate but interacting systems: a visual system for representing the structure of an observed object, and a semantic system that mediates recognition and also permits retrieval of other information about familiar kinds of objects. The former system is engaged by any visually presented object, regardless of its authenticity, but is shaped by experience so that the frequency with which object features co-occur is reflected in the amplitude of the early brain response. Authentic items, because they are associated with a fairly rich constellation of conceptual information, efficiently engage the semantic system in later time ranges. At intermediate latencies, information from both the perceptual and the semantic system is integrated in an interactive process, giving rise to the interaction of typicality and authenticity in the ERP signal.

### Relationship to Visual Word Recognition

In some respects, it is remarkable how closely the present results match our previous ERP investigation of visual word recognition (Hauk et al., 2006). That study, like the current one, employed a yes/no recognition task with visual stimuli (written words and pseudowords) that orthogonally varied structural typicality (specifically, the positional bigram and trigram frequencies of the letter strings) and authenticity (i.e., lexicality). As in the present work, we observed an early effect of structural typicality that did not interact with authenticity; a later main effect of authenticity that did not interact with typicality; and an interaction between these factors at an intermediate latency. Of particular interest,

the timing of the early main effect of structural typicality was nearly identical in the two studies (near 100 msec), possibly indicating the operation of a shared visual process in the two tasks that is sensitive to correlational structure among visual properties, whether of object features or printed letters.

We also observed some interesting differences from the previous study. Perhaps most striking was the main effect of typicality on response times (faster responses for atypical items) in the present work, which was not observed in visual word recognition. This pattern may reflect key differences in the structure of orthographic versus object representations and their relationship to semantic representations. Specifically, visual object recognition is a complex process composed of object feature perception and integration; prominent features of atypical objects are frequently associated with a single concept (or a small number of concepts)—as, for instance, a trunk is associated with an elephant, or a crest with a rooster—so that the presence of the attribute strongly constrains the other visual properties that must be present if the item is to be judged familiar. The rapid responses observed for atypical items in the current study may capitalize on such systematic part-whole relationships. The components of written words—individual letters—are never so systematically linked to individual concepts. To the contrary, small changes to a single letter in a word usually betoken a completely different concept, so that all components of a word must be considered together to support a lexical decision. Consequently, structurally unusual words show no advantage in the recognition task.

A second interesting difference from the previous study concerns the source estimates for the various effects. In word recognition, the early-occurring effect of typicality and the later-occurring effect of authenticity derived from near-identical sources in the left posterior/inferior temporal cortex, whereas the interaction derived from a left anterior temporal lobe source. In the present study, source estimates are consistent with the notion that an earlier visual representation (sensitive to typicality) gives way to a later semantic representation (sensitive to authenticity), and that these representations are coded by cortical regions with little overlap.

### Relationship to Behavioral Patient Data

We noted in the Introduction that patients with semantic impairments following anterior temporal lobe atrophy are markedly impaired in both word and object recognition tasks, and that they increasingly come to prefer typically structured stimuli as real items for both tasks, regardless of whether such items correspond to authentic words or objects (Patterson et al., 2006). From these observations, we have proposed that, when targets and foils are matched for their structural characteristics, successful recognition depends upon semantic



processing sustained in part by anterior temporal lobe regions. The current data are consistent with this hypothesis: The main ERP effect of authenticity was associated with activation along the lateral/inferior extent of the temporal lobes bilaterally as far anterior as the pole. Disruption of this activation from anterior temporal lobe pathology may, therefore, erode the signal that permits successful recognition, leading patients to rely more heavily upon the earlier-occurring perceptual processes that discriminate typical from atypical items but are not sensitive to authenticity.

We do not imply that the temporal lobes are the only cortical areas that contribute to semantic processes. Information about the meanings of words and objects is known to be widely distributed across the brain, with the patterns of such representation partially modulated by specific object categories (Pulvermüller, 2005; Caramazza & Mahon, 2003; Martin & Chao, 2001). Temporal lobe regions are, however, known to play a crucial role in linking visual input patterns to semantic representations of objects, and anterior and middle temporal lobe pathology is known to produce semantic impairment from a variety of etiologies (Hart & Gordon, 1990; Alexander, Hiltbrunner, & Fischer, 1989; Kertesz, Sheppard, & MacKenzie, 1982)—and these were the re-

gions associated with the “recognition” signal in the current study.

## Conclusions

The most important novel contribution of our study is its demonstration of the large impact of structural typicality on object recognition. The title of our article is, of course, a play on the title of the famous short story by Rudyard Kipling (“How the Camel Got its Hump”). This fable, in which the camel is “saddled” with a hump as a punishment for being lazy, emphasizes in a fantastical way how atypical the hump is. In our post-Darwinian world, we have a more rational view of why camels are humped, but an understanding of their origin does not make humped backs any less atypical. There is accruing evidence, mainly from the study of patients with SD, that when a relatively intact perceptual analysis system is forced to interact with a degraded rather than a normal semantic system, typicality comes to play the dominant role in object processing. The current study provides the first evidence in healthy individuals for the impact of this important factor of typicality on early stages of object processing and for its electrophysiological correlates.

## APPENDIX: LIST OF STIMULUS ITEMS

F = mean familiarity rating.

<i>Authentic Typical</i>	<i>F</i>	<i>Nonauthentic Typical, Description</i>	<i>F</i>	<i>Authentic Atypical</i>	<i>F</i>	<i>Nonauthentic Atypical, Description</i>	<i>F</i>
Airplane	5.0	Triplane w/ 747 wings	1.6	Triplane	3.4	747 w/ triplane wings	1.9
Alligator	3.9	Octopus w/ alligator body and legs	1.0	Octopus	3.7	Alligator w/ octopus body and legs	1.1
Axe	5.7	Scissors w/ axe handle	1.5	Scissors	6.8	Axe w/ scissor handles	1.3
Baboon	4.1	Caribou w/ baboon head	1.0	Caribou	4.4	Baboon w/ caribou head	1.4
Beaver	3.2	Parrot w/ beaver face and mouth	1.0	Parrot	4.6	Beaver w/ parrot face and beak	1.3
Buffalo	4.3	Armadillo w/ buffalo body	1.1	Armadillo	3.9	Buffalo w/ armadillo body	1.3
Bus	6.3	Boat w/ bus undercarriage	1.8	Boat	4.6	Bus w/ boat undercarriage	1.2
Cheetah	4.3	Goose w/ cheetah legs	1.3	Goose	5.0	Cheetah w/ goose legs	1.3
Chicken	5.8	Flamingo w/ chicken legs and short neck	1.4	Flamingo	3.8	Chicken w/ flamingo legs and long neck	2.1
Chipmunk	4.0	Chameleon w/ chipmunk head	1.2	Chameleon	2.9	Chipmunk w/ chameleon head	1.3
Chisel	5.4	Clothes peg w/ chisel handle	1.8	Clothes peg	6.3	Chisel w/ clothes peg handles	1.5
Coyote	4.9	Aardvark w/ coyote head	1.5	Aardvark	2.6	Coyote w/ aardvark head	1.7
Crocodile	3.9	Fish w/ crocodile legs	1.4	Fish	5.5	Crocodile w/ fish fins and no legs	1.3
Deer	4.6	Duck w/ 4 legs	1.5	Duck	5.9	Deer w/ 6 legs	1.0
Ferret	2.5	Killer whale w/ ferret legs	1.2	Killer whale	4.2	Ferret w/ killer whale fins and no legs	1.0
Flatbed	4.5	Helicopter w/ flatbed undercarriage	1.0	Helicopter	5.5	Flatbed w/ helicopter undercarriage	1.3

# APPENDIX (continued)

<i>Authentic Typical</i>	<i>F</i>	<i>Nonauthentic Typical, Description</i>	<i>F</i>	<i>Authentic Atypical</i>	<i>F</i>	<i>Nonauthentic Atypical, Description</i>	<i>F</i>
Fork	7.0	Comb w/ handle added	1.3	Comb	6.9	Fork w/ no handle	2.5
Fox	5.1	Eagle w/ fox head	1.3	Eagle	4.7	Fox w/ eagle head	1.3
Gecko	2.3	Dolphin w/ gecko legs	1.0	Dolphin	4.1	Gecko w/ dolphin fins and no legs	1.4
Giraffe	4.3	Seahorse w/ giraffe body and legs	1.1	Seahorse	4.0	Giraffe w/ body and tail	1.0
Goat	4.9	Rooster w/ goat body and legs	1.0	Rooster	5.6	Goat w/ rooster body and legs	1.0
Gray squirrel	5.4	Frog w/ gray squirrel legs and tail	1.0	Frog	5.0	Gray squirrel w/ frog legs	1.0
Ground squirrel	3.3	Sea turtle w/ ground squirrel legs	1.0	Sea turtle	2.7	Ground squirrel w/ sea turtle fins and no legs	1.0
Hammer	6.3	Pliers w/ hammer handle	1.8	Pliers	5.9	Hammer w/ plier handles	1.5
Hedgehog	4.8	Tortoise w/ hedgehog body	1.4	Tortoise	4.4	Hedgehog w/ tortoise body (shell)	1.4
Hippo	2.8	Walrus w/ hippo body and legs	1.3	Walrus	3.8	Hippo w/ walrus body and legs	1.0
Hyena	3.3	Platypus w/ hyena head	1.3	Platypus	3.3	Hyena w/ platypus head	1.1
Jackal	3.6	Camel w/ jackal back	1.6	Camel	4.8	Jackal w/ camel hump	1.8
Jalopy	4.7	Blimp w/ jalopy undercarriage	1.1	Blimp	3.1	Jalopy w/ blimp undercarriage	1.1
Jumping mouse	3.6	Pigeon w/ jumping mouse legs	1.8	Pigeon	5.9	Jumping mouse w/ pigeon feet	1.3
Kangaroo	4.5	Penguin w/ kangaroo head	1.0	Penguin	3.9	Kangaroo w/ penguin head	1.3
Lion	4.2	Ostrich w/ lion tail	2.1	Ostrich	3.6	Lion w/ ostrich tail	1.8
Manatee	3.5	Swordfish w/ manatee head	1.5	Swordfish	3.3	Manatee w/ swordfish head	1.2
Monkey	4.5	Elephant w/ monkey face	1.0	Elephant	4.8	Monkey w/ elephant face and trunk	1.0
Moose	3.5	Bear w/ moose head	1.3	Bear	4.4	Moose w/ bear head	1.0
Mouse	4.7	Rabbit w/ mouse head	2.3	Rabbit	5.8	Mouse w/ rabbit head	2.3
Newt	4.3	Cricket w/ newt legs	1.0	Cricket	3.6	Newt w/ cricket legs	1.0
Panda	4.4	Koala w/ panda head	2.4	Koala	3.9	Panda w/ koala head	2.0
Pig	5.5	Bird w/ pig head	1.0	Bird	6.5	Pig w/ bird head	1.3
Prairie dog	3.3	Puffin w/ prairie dog face and mouth	1.3	Puffin	3.4	Prairie dog w/ puffin face and beak	1.3
Raccoon	2.4	Turtle w/ raccoon head	1.2	Turtle	4.8	Raccoon w/ turtle head	1.1
Racket	5.9	Umbrella w/ racket handle as top	1.5	Umbrella	6.1	Racket w/ umbrella top	1.3
Screwdriver	6.3	Spanner w/ screwdriver handle	2.0	Spanner	4.5	Screwdriver w/ spanner handle	2.7
Sheep	4.3	Seal w/ sheep legs	1.1	Seal	3.9	Sheep w/ seal body and fins	1.3
Spade	6.1	Scythe w/ spade handle	1.6	Scythe	4.4	Spade w/ scythe handle	1.7
Squid	3.7	Whale w/ squid tentacles	1.3	Whale	4.0	Squid w/ whale body and tail	1.4
Toad	3.7	Swan w/ toad legs	1.1	Swan	6.1	Toad w/ swan body and no legs	1.0
Tram	3.6	Chinook w/ tram top	1.1	Hinook	3.3	Tram w/ Chinook top	1.7
Truck	6.4	Train w/ truck undercarriage	3.8	Train	5.0	Truck w/ train undercarriage	2.0
Weasel	4.3	Anteater w/ weasel head	1.8	Anteater	3.4	Weasel w/ anteater head	2.1
Avg rating	4.5		1.6		4.5		1.4

## Acknowledgments

The contribution of three of the authors (K. P., A. W., and E. P.) to this project was supported in full or in part by National Institutes of Mental Health IBSC Grant MH64445. We thank Lawrence Watling for his help in creating the picture stimuli, and Markus Junghöfer for advice on stimulus matching.

Reprint requests should be sent to Olaf Hauk, MRC-CBU, 15 Chaucer Road, Cambridge CB2 7EF, UK, or via e-mail: olaf.hauk@mrc-cbu.cam.ac.uk; Tim Rogers, Department of Psychology, University of Wisconsin-Madison, Madison, WI 53706, USA, or via e-mail: ttrgers@wisc.edu.

## REFERENCES

- Alexander, M. P., Hiltbrunner, B., & Fischer, R. S. (1989). Distributed anatomy of transcortical sensory aphasia. *Archives of Neurology*, 46, 885–892.
- Barrett, S. E., & Rugg, M. D. (1990). Event-related potentials and the semantic matching of pictures. *Brain and Cognition*, 14, 201–212.
- Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological Review*, 94, 115–147.
- Bullier, J. (2001). Integrated model of visual processing. *Brain Research, Brain Research Reviews*, 36, 96–107.
- Caramazza, A., & Mahon, B. Z. (2003). The organization of conceptual knowledge: The evidence from category-specific semantic deficits. *Trends in Cognitive Sciences*, 7, 354–361.
- Dale, A. M., & Sereno, M. I. (1993). Improved localization of cortical activity by combining EEG and MEG with MRI cortical surface reconstruction: A linear approach. *Journal of Cognitive Neuroscience*, 5, 162–176.
- Eulitz, C., Hauk, O., & Cohen, R. (2000). Electroencephalographic activity over temporal brain areas during phonological encoding in picture naming. *Clinical Neurophysiology*, 111, 2088–2097.
- Gerlach, C. (2001). Structural similarity causes different category-effects depending on task characteristics. *Neuropsychologia*, 39, 895–900.
- Gerlach, C., Law, I., Gade, A., & Paulson, O. B. (1999). Perceptual differentiation and category effects in normal object recognition: A PET study. *Brain*, 122, 2159–2170.
- Greenhouse, S. W., & Geisser, S. (1959). On methods in the analysis of profile data. *Psychometrika*, 55, 431–433.
- Grill-Spector, K. (2003). The neural basis of object perception. *Current Opinion in Neurobiology*, 13, 159–166.
- Grill-Spector, K., & Kanwisher, N. (2005). Visual recognition: As soon as you know it is there, you know what it is. *Psychological Science*, 16, 152–160.
- Halgren, E., Raij, T., Marinkovic, K., Jousmaki, V., & Hari, R. (2000). Cognitive response profile of the human fusiform face area as determined by MEG. *Cerebral Cortex*, 10, 69–81.
- Hämäläinen, M. S., & Ilmoniemi, R. J. (1994). Interpreting magnetic fields of the brain: Minimum norm estimates. *Medical & Biological Engineering & Computing*, 32, 35–42.
- Hart, J., Jr., & Gordon, B. (1990). Delineation of single-word semantic comprehension deficits in aphasia, with anatomical correlation. *Annals of Neurology*, 27, 226–231.
- Hauk, O. (2004). Keep it simple: A case for using classical minimum norm estimation in the analysis of EEG and MEG data. *Neuroimage*, 21, 1612–1621.
- Hauk, O., Patterson, K., Woollams, A., Watling, L., Pulvermüller, F., & Rogers, T. T. (2006). [Q:] When would you prefer a SOSSAGE to a SAUSAGE? [A:] At about 100 msec. ERP correlates of orthographic typicality and lexicality in written word recognition. *Journal of Cognitive Neuroscience*, 18, 818–832.
- Hauk, O., Rockstroh, B., & Eulitz, C. (2001). Grapheme monitoring in picture naming: An electrophysiological study of language production. *Brain Topography*, 14, 3–13.
- Hillis, A. E., & Caramazza, A. (1995). Cognitive and neural mechanisms underlying visual and semantic processing: Implications from “optic aphasia.” *Journal of Cognitive Neuroscience*, 7, 457–478.
- Hodges, J. R., & Patterson, K. (1996). Nonfluent progressive aphasia and semantic dementia: A comparative neuropsychological study. *Journal of the International Neuropsychological Society*, 2, 511–524.
- Hodges, J. R., Patterson, K., Oxbury, S., & Funnell, E. (1992). Semantic dementia. Progressive fluent aphasia with temporal lobe atrophy. *Brain*, 115, 1783–1806.
- Holcomb, P. J., & McPherson, W. B. (1994). Event-related brain potentials reflect semantic priming in an object decision task. *Brain and Cognition*, 24, 259–276.
- Hovius, M., Kellenbach, M. L., Graham, K. S., Hodges, J. R., & Patterson, K. (2003). What does the object decision task measure? Reflections on the basis of evidence from semantic dementia. *Neuropsychology*, 17, 100–107.
- Humphreys, G. W., & Forde, E. M. (2001). Hierarchies, similarity, and interactivity in object recognition: “Category-specific” neuropsychological deficits. *Behavioral and Brain Sciences*, 24, 453–476; discussion 476–509.
- Humphreys, G. W., Lamote, C., & Lloyd-Jones, T. J. (1995). An interactive activation approach to object processing: Effects of structural similarity, name frequency, and task in normality and pathology. *Memory*, 3, 535–586.
- Humphreys, G. W., & Riddoch, M. J. (1987). *To see but not to see: Case study of visual agnosia*. Hove, UK: Psychology Press, Taylor & Francis group.
- Johnson, J. S., & Olshausen, B. A. (2005). The earliest EEG signatures of object recognition in a cue-target task are postsensory. *Journal of Vision*, 5, 299–312.
- Jolicoeur, P., Gluck, M. A., & Kosslyn, S. M. (1984). Pictures and names: Making the connection. *Cognitive Psychology*, 16, 243–275.
- Kellenbach, M. L., Hovius, M., & Patterson, K. (2005). A pet study of visual and semantic knowledge about objects. *Cortex*, 41, 121–132.
- Kertesz, A., Sheppard, A., & MacKenzie, R. (1982). Localization in transcortical sensory aphasia. *Archives of Neurology*, 39, 475–478.
- Kiefer, M. (2001). Perceptual and semantic sources of category-specific effects: Event-related potentials during picture and word categorization. *Memory & Cognition*, 29, 100–116.
- Kutas, M., & Federmeier, K. D. (2000). Electrophysiology reveals semantic memory use in language comprehension. *Trends in Cognitive Sciences*, 4, 463–470.
- Levelt, W. J. (1995). *Speaking: From intention to articulation*. Cambridge: MIT Press.
- Levelt, W. J., Praamstra, P., Meyer, A. S., Helenius, P., & Salmelin, R. (1998). An MEG study of picture naming. *Journal of Cognitive Neuroscience*, 10, 553–567.
- Lloyd-Jones, T. J., & Luckhurst, L. (2002a). Effects of plane rotation, task, and complexity on recognition of familiar and chimeric objects. *Memory & Cognition*, 30, 499–510.
- Lloyd-Jones, T. J., & Luckhurst, L. (2002b). Outline shape is a mediator of object recognition that is particularly important for living things. *Memory & Cognition*, 30, 489–498.

- Marr, D., & Nishihara, H. K. (1978). Representation and recognition of the spatial organization of three-dimensional shapes. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, 200, 269–294.
- Martin, A., & Chao, L. L. (2001). Semantic memory and the brain: Structure and processes. *Current Opinion in Neurobiology*, 11, 194–201.
- Michel, C. M., Seeck, M., & Murray, M. M. (2004). The speed of visual cognition. *Clinical Neurophysiology Supplement*, 57, 617–627.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9, 97–113.
- Patterson, K., Lambon Ralph, M. A., Jefferies, E., Woollams, A., Jones, R., Hodges, J. R., et al. (2006). “Presemantic” cognition in semantic dementia: Six deficits in search of an explanation. *Journal of Cognitive Neuroscience*, 18, 169–183.
- Price, C. J. (2000). The anatomy of language: Contributions from functional neuroimaging. *Journal of Anatomy*, 197, 335–359.
- Pulvermüller, F. (2001). Brain reflections of words and their meaning. *Trends in Cognitive Sciences*, 5, 517–524.
- Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, 6, 576–582.
- Riddoch, M. J., & Humphreys, G. W. (1987). Visual object processing in optic aphasia: A case of semantic access agnosia. *Cognitive Neuropsychology*, 4, 131–185.
- Riddoch, M. J., & Humphreys, G. W. (1993). *BORB: Birmingham Object Recognition Battery*. Hillsdale, NJ: Erlbaum.
- Rogers, T. T., Lambon Ralph, M. A., Garrard, P., Bozeat, S., McClelland, J. L., Hodges, J. R., et al. (2004). Structure and deterioration of semantic memory: A neuropsychological and computational investigation. *Psychological Review*, 111, 205–235.
- Rogers, T. T., Lambon Ralph, M. A., Hodges, J., & Patterson, K. (2003). Object recognition under semantic impairment: The effects of conceptual regularities on perceptual decisions. *Language and Cognitive Processes*, 18, 625–662.
- Rogers, T. T., Lambon Ralph, M. A., Hodges, J. R., & Patterson, K. (2004). Natural selection: The impact of semantic impairment on lexical and object decision. *Cognitive Neuropsychology*, 21, 331–352.
- Rossion, B., Joyce, C. A., Cottrell, G. W., & Tarr, M. J. (2003). Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. *Neuroimage*, 20, 1609–1624.
- Salmelin, R., Hari, R., Lounasmaa, O. V., & Sams, M. (1994). Dynamics of brain activation during picture naming. *Nature*, 368, 463–465.
- Schendan, H. E., Ganis, G., & Kutas, M. (1998). Neurophysiological evidence for visual perceptual categorization of words and faces within 150 ms. *Psychophysiology*, 35, 240–251.
- Schmitt, B. M., Munte, T. F., & Kutas, M. (2000). Electrophysiological estimates of the time course of semantic and phonological encoding during implicit picture naming. *Psychophysiology*, 37, 473–484.
- Sitnikova, T., West, W. C., Kuperberg, G. R., & Holcomb, P. J. (2006). The neural organization of semantic memory: Electrophysiological activity suggests feature-based segregation. *Biological Psychology*, 71, 326–340.
- Snowden, J. S., Neary, D., Mann, D. M., Goulding, P. J., & Testa, H. J. (1992). Progressive language disorder due to lobar atrophy. *Annals of Neurology*, 31, 174–183.
- VanRullen, R., & Thorpe, S. J. (2001). The time course of visual processing: From early perception to decision-making. *Journal of Cognitive Neuroscience*, 13, 454–461.