Early Visual Word Processing Is Flexible: Evidence from Spatiotemporal Brain Dynamics

Yuanyuan Chen¹,², Matthew H. Davis², Friedemann Pulvermüller²,³, and Olaf Hauk²

Abstract

Visual word recognition is often described as automatic, but the functional locus of top-down effects is still a matter of debate. Do task demands modulate how information is retrieved, or only how it is used? We used EEG/MEG recordings to assess whether, when, and how task contexts modify early retrieval of specific psycholinguistic information in occipito-temporal cortex, an area likely to contribute to early stages of visual word processing. Using a parametric approach, we analyzed the spatiotemporal response patterns of occipitotemporal cortex for orthographic, lexical, and semantic variables in three psycholinguistic tasks: silent reading, lexical decision, and semantic decision. Task modulation of word frequency and imageability effects occurred simultaneously in ventral occipito-temporal regions—in the vicinity of the putative visual word form area—around 160 msec, following task effects on orthographic typicality around 100 msec. Frequency and typicality also produced task-independent effects in anterior temporal lobe regions after 200 msec. The early task modulation for several specific psycholinguistic variables indicates that occipitotemporal areas integrate perceptual input with prior knowledge in a task-dependent manner. Still, later task-independent effects in anterior temporal lobes suggest that word recognition eventually leads to retrieval of semantic information irrespective of task demands. We conclude that even a highly overlearned visual task like word recognition should be described as flexible rather than automatic.

INTRODUCTION

The investigation of putative top-down effects on perception has a long history in cognitive science (Treisman, 1969; Deutsch & Deutsch, 1963). Printed words are an interesting special case, because they are complex visual objects, with an arbitrary form-to-meaning relationship that is usually acquired over several years during childhood (Dehaene, 2009). According to some authors, “one of the oldest debates in visual word recognition concerns the demarcation between bottom-up and top-down processing” (Carreiras, Armstrong, Perea, & Frost, 2014). It has been claimed that the field has suffered from the “curse of automaticity,” that is, the strong view that early word recognition processes are automatic and not systematically affected by task demands (Balota & Yap, 2006). However, even behavioral benchmark findings such as the word frequency effect (faster responses for more familiar words) depend on the task (Balota & Yap, 2006; Balota, Cortese, Sergent-Marshall, Spieler, & Yap, 2004), and task effects on unconscious masked semantic priming have been reported (Kiefer & Martens, 2010; Norris & Kinoshita, 2008). Computational models of word recognition agree that task effects reflect different use of information (Norris, 2006; Ratcliff, Gomez, & McKoon, 2004; Grainger & Jacobs, 1996) but do not specify whether task context affects the retrieval of information. Do task demands modulate how information is retrieved at the earliest stages of information retrieval or only how it is used after an automatic retrieval stage? Empirically distinguishing these alternatives requires the separation of the earliest lexico-semantic information retrieval from later recurrent activation or postrecognition processes.

In the neuroscientific literature, early visual word recognition is commonly associated with processing in left ventral temporal cortex, whose role in general complex visual processing is well established (Lamme & Roelfsema, 2000). However, important questions about the stimulus and task parameters that modulate these processes are still unanswered, in particular to what degree a distinction between “retrieval” and “decision-making” is neurophysiologically meaningful. A particular area in ventral occipitotemporal cortex, labeled the “visual word form area” (VWFA), has been associated with strictly visual and prelexical feedforward processing in the context of the Local Combination Detector Model (Dehaene & Cohen, 2011; Cohen et al., 2000). Price and Devlin’s Interactive Account assumes that the function of occipitotemporal cortex “involves the synthesis of bottom-up sensory input with top-down predictions that are generated automatically.
from prior experience” (Price & Devlin, 2011). Studying the spatiotemporal dynamics of brain activation in inferior temporal cortex during visual word processing is therefore crucial to reveal the nature of early top–down effects.

What exactly is “early” is still debated in the literature. Although some authors have focused on the N400 time window with respect to lexico-semantic processing (Kutas & Federmeier, 2011; Lau, Phillips, & Poeppel, 2008) and, for example, have associated a P325 with lexical access (Grainger & Holcomb, 2009), others have claimed that lexico-semantic processing already happens within the first 200 msec (Pulvermuller, Shtyrov, & Hauk, 2009). In the object recognition literature, categorization of complex object categories has been reported to occur about 150 msec after stimulus onset (Fabre-Thorpe, Delorme, Marlot, & Thorpe, 2001) or even earlier (Kirchner & Thorpe, 2006). Two recent studies converged on the view that lexico-semantic information retrieval is already under way around 160 msec following visual word presentation (Amsel, Urbach, & Kutas, 2013; Hauk, Coutout, Holden, & Chen, 2012). Thus, systematic task effects in this latency range independent of general attentional load would be clear evidence that early lexico-semantic information retrieval is not automatic.

Already based on task effects in behavioral data, Balota and Yap (2006) proposed their “flexible lexical processors” model, suggesting that word processing is adaptive to task demands at multiple stages. Unfortunately, behavioral data are unable to decide whether task effects occur at early or late stages of processing. Masked priming effects in ERP data have been used to argue in favor of automatic and unconscious word processing (Dehaene et al., 2004; Neely & Kahan, 2001). However, even masked semantic priming ERP effects have been shown to depend on the task context (Kiefer & Martens, 2010). In the latter study, the masked semantic priming effect on the N400 amplitude was smaller when trials were preceded by a perceptual task compared to a semantic task. The authors explained their findings using their “attentional sensitization” model, which assumes that unconscious processes can be enhanced or diminished depending on task goals. Although this indicates that unconscious processing can be affected by top–down control, it is still not clear whether task demands affected information retrieval from the masked prime or the way this information affected target word processing. Any process leading to the N400 of the target word may have been responsible for the effect.

A number of previous studies investigating top–down effects on word recognition have either studied task effects using slow neuroimaging techniques such as fMRI (Harel, Kravitz, & Baker, 2014; Twomey, Kawabata Duncan, Price, & Devlin, 2011; Glezer, Jiang, & Riesenhuber, 2009; Vinckier et al., 2007; Sabsevitz et al., 2005; Kronbichler et al., 2004) or used surface ERPs and did not perform source analysis (Strijkers, Bertrand, & Grainger, 2015; Strijkers, Yun, Grainger, & Holcomb, 2011; Ruiz & Nobre, 2008; Bentin, Mouchetant-Rostaing, Giard, Echallier, & Peron, 1999). Here, we used combined EEG/MEG and distributed source estimation to track the time course of brain activation in left ventral temporal cortex during visual word recognition under different task demands. We used three tasks that required processing of letter strings at a linguistic level, namely lexical decision, semantic decision, and silent reading. These are standard tasks in the behavioral literature, where, for example, lexical or semantic decision button press latencies have been compared with voice onset times (VOTs) in overt naming (Balota et al., 2004).

Importantly, we did not just test for task effects on general word activation as in some previous studies (Chen, Davis, Pulvermuller, & Hauk, 2013; Strijkers et al., 2011; Bentin et al., 1999) but investigated task effects on specific psycholinguistic variables associated with different aspects of the word recognition process: orthographic typicality, word frequency, and imageability. These variables have been shown to activate parts of the ventral temporal cortex in several previous studies (Woodlams, Silani, Okada, Patterson, & Price, 2011; Hauk, Davis, & Pulvermuller, 2008; Sabsevitz et al., 2005; Kronbichler et al., 2004). The exact pattern of early effects for specific psycholinguistic variables is still not established in the literature, and effect sizes can be expected to be small. Thus, we employed sensitive analysis procedures to make optimal use of the available information and applied linear multiple regression analysis to extract effects of psycholinguistic variables from our EEG and MEG signals (Smith & Kutas, 2015; Miozzo, Pulvermuller, & Hauk, 2014; Hauk, Pulvermuller, Ford, Marslen-Wilson, & Davis, 2009; Hauk, Davis, Ford, Pulvermuller, & Marslen-Wilson, 2006). Furthermore, we restricted our analysis on left ventral temporal cortex, a cortical structure most likely involved in early visual word processing (Taylor, Rastle, & Davis, 2013; Dehaene & Cohen, 2011; Price & Devlin, 2011), and used an ROI-based analysis similar to the one of Vinckier et al. (2007) applied to fMRI data.

Our predictions for the general time course of psycholinguistic EEG/MEG effects were based on our previous work (Hauk et al., 2009; Pulvermuller et al., 2009; Hauk, Davis, et al., 2006; Hauk, Patterson, et al., 2006). We expected orthographic typicality effects around 100 msec, and lexico-semantic effects to start around 150 msec. Any task effects at these early latencies would demonstrate top–down modulation of word recognition processes at the earliest stages. This interpretation would be strengthened if we could demonstrate systematic differences in the localization of these effects with respect to task. The word frequency effect, arguably the most established psycholinguistic effect in the behavioral literature on visual word recognition, has been shown to be larger in lexical decision compared with other tasks (Balota & Yap, 2006; Balota et al., 2004). It has been argued that this is because lexical decisions are based on a measure of “wordlikeness” (Norris, 2009; Grainger & Jacobs, 1996), which is at least partly derived from orthographic similarity to other words, and in particular whole-word frequency. We therefore expect larger task effects on our orthographic
and lexical variables in the lexical decision tasks in visual cortex and around the putative VWFA (Woodlams et al., 2011; Hauk, Davis, & Pulvermuller, 2008).

Our semantic task may produce larger modulation of the effects for the semantic variable imageability. We can expect two possible patterns: Imageability may modulate activity in amodal semantic areas, such as the anterior temporal lobe (Patterson, Nestor, & Rogers, 2007), or it may be reflected in visual areas in line with embodied theories of semantics (Pulvermuller, 2013; Hauk, Davis, Kherif, & Pulvermuller, 2008). We also included a silent reading task, which is closer to the way people read natural text and to reading aloud in the experimental literature. Thus, this task should emphasize phonological and possibly inhibited articulatory processes, consistent with precentral activation for this task in a previous analysis (Chen et al., 2013). Although we do not have specific predictions for activation patterns along the ventral temporal cortex, topographic differences among these three tasks would provide novel evidence for task modulation of early word recognition processes.

METHODS

Participants

We here report results from fifteen participants (11 women). A further three participants were tested, but data were discarded because of excessive body and eye movement artifacts. Some results for this data set have already been reported in a previous study, which are independent of the present analysis (Chen et al., 2013). All participants were right-handed (mean laterality quotient of 86.9 (SD = 18.4; Oldfield, 1971), were on average 25 years old (SD = 5.6 years), and had 16.6 years of formal education. All participants were native English speakers and had normal or corrected-to-normal vision, and none of them reported having any neurological disorder or dyslexia. They were paid £10 per hour (£20 minimum) for their participation. The experiment was approved by the Cambridge Psychology research ethics committee.

Stimuli and Psycholinguistic Variables

Six hundred content words (200 per task) were selected for the experiment from the MRC Psycholinguistic Database, with word lengths between three and seven letters, word form and lemma frequency per million greater than 0, and they were not listed as morphologically complex in the CELEX database (Baayen, Piepenbrock, & van Rijn, 1993). Bigram frequency, trigram frequency, word length, word form frequency, lemma frequency, and neighborhood size (N) were obtained from CELEX database (Baayen et al., 1993). Concreteness and imageability were obtained from the MRC Psycholinguistic Database. We computed two further semantic covariates for these items: number of senses and meanings from the Wordsmyth database (www.wordsmyth.net/) and action relatedness using the rating procedure from Hauk, Davis, Kherif, et al. (2008), but given our focus on variables that impact on ventral temporal activity, these variables will not be considered in our EEG/MEG results.

Stimuli were divided into three lists, matched on all the variables mentioned above using the Match software (van Casteren & Davis, 2007; see Table 1). Word lists were counterbalanced over tasks for different participants to ensure that item-specific effects cannot contribute to observed task effects. Two hundred pseudowords were created for the lexical decision task. They were matched with the three word lists for word length, bigram frequency, trigram frequency, and neighborhood size (N). Twenty common person’s names (e.g., Jack, Mandy) were used as target trials in the semantic decision

Table 1. Descriptive Statistics for Stimuli

<table>
<thead>
<tr>
<th></th>
<th>Word List 1</th>
<th>Word List 2</th>
<th>Word List 3</th>
<th>Pseudowords</th>
</tr>
</thead>
<tbody>
<tr>
<td>Word length</td>
<td>5.03 (1.1)</td>
<td>5.05 (1.04)</td>
<td>4.9 (0.89)</td>
<td>4.86 (0.79)</td>
</tr>
<tr>
<td>Bigram</td>
<td>32882.39 (12136.29)</td>
<td>33855.98 (15335.4)</td>
<td>34113.87 (13828.06)</td>
<td>34392.19 (14063)</td>
</tr>
<tr>
<td>Trigram</td>
<td>3568.2 (2195.92)</td>
<td>3509.98 (2244.32)</td>
<td>3394.78 (2218.53)</td>
<td>3346.39 (2155.28)</td>
</tr>
<tr>
<td>N</td>
<td>4.07 (4.29)</td>
<td>4.17 (4.21)</td>
<td>4.2 (4.12)</td>
<td>4.21 (4.05)</td>
</tr>
<tr>
<td>Word form frequency</td>
<td>41.92 (76.59)</td>
<td>44.01 (75.69)</td>
<td>42.62 (73.91)</td>
<td>N/A</td>
</tr>
<tr>
<td>Lemma frequency</td>
<td>80.14 (143.67)</td>
<td>88.06 (204.32)</td>
<td>72.44 (112.21)</td>
<td>N/A</td>
</tr>
<tr>
<td>Concreteness</td>
<td>511.19 (107.62)</td>
<td>514.99 (97.89)</td>
<td>517.81 (105.73)</td>
<td>N/A</td>
</tr>
<tr>
<td>Imageability</td>
<td>524.69 (86.01)</td>
<td>527.9 (81.51)</td>
<td>529.33 (84.18)</td>
<td>N/A</td>
</tr>
<tr>
<td>Action relatedness</td>
<td>3.31 (0.95)</td>
<td>3.32 (0.94)</td>
<td>2.82 (1.2)</td>
<td>N/A</td>
</tr>
<tr>
<td>Number of meanings</td>
<td>1.15 (0.4)</td>
<td>1.19 (0.51)</td>
<td>1.18 (0.45)</td>
<td>N/A</td>
</tr>
<tr>
<td>Number of senses</td>
<td>4.62 (3.06)</td>
<td>4.96 (3.14)</td>
<td>5.15 (3)</td>
<td>N/A</td>
</tr>
</tbody>
</table>

Mean (SD) for the raw psycholinguistic variables for the three word lists and one pseudoword list.
Table 2. Pairwise Correlations between Raw Variables (First Column) and Six PCA Factors (First Row) That Were Entered into Regression Analysis

<table>
<thead>
<tr>
<th></th>
<th>Length/N</th>
<th>Bi/Trigram</th>
<th>Frequency</th>
<th>Imageability</th>
<th>Action</th>
<th>N.MeanSenses</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length</td>
<td>0.91</td>
<td>0.27</td>
<td>−0.07</td>
<td>−0.07</td>
<td>−0.04</td>
<td>−0.22</td>
</tr>
<tr>
<td>N</td>
<td>−0.91</td>
<td>−0.11</td>
<td>0.09</td>
<td>0.16</td>
<td>0.10</td>
<td>0.34</td>
</tr>
<tr>
<td>Bigram</td>
<td>0.19</td>
<td>0.88</td>
<td>0.13</td>
<td>−0.11</td>
<td>−0.06</td>
<td>−0.03</td>
</tr>
<tr>
<td>Trigram</td>
<td>0.18</td>
<td>0.88</td>
<td>0.12</td>
<td>−0.08</td>
<td>0.02</td>
<td>−0.04</td>
</tr>
<tr>
<td>WordFre</td>
<td>−0.04</td>
<td>0.15</td>
<td>0.96</td>
<td>−0.09</td>
<td>0.11</td>
<td>0.09</td>
</tr>
<tr>
<td>LemFre</td>
<td>−0.13</td>
<td>0.13</td>
<td>0.96</td>
<td>−0.11</td>
<td>0.27</td>
<td>0.27</td>
</tr>
<tr>
<td>CNC</td>
<td>−0.13</td>
<td>−0.11</td>
<td>−0.13</td>
<td>0.97</td>
<td>0.02</td>
<td>0.04</td>
</tr>
<tr>
<td>IMG</td>
<td>−0.11</td>
<td>−0.10</td>
<td>−0.07</td>
<td>0.97</td>
<td>0.05</td>
<td>0.02</td>
</tr>
<tr>
<td>Action</td>
<td>−0.08</td>
<td>−0.02</td>
<td>0.19</td>
<td>0.03</td>
<td>1.00</td>
<td>0.14</td>
</tr>
<tr>
<td>N.Mean</td>
<td>−0.33</td>
<td>−0.09</td>
<td>−0.01</td>
<td>0.08</td>
<td>0.02</td>
<td>0.83</td>
</tr>
<tr>
<td>N.Senses</td>
<td>−0.18</td>
<td>0.02</td>
<td>0.32</td>
<td>−0.03</td>
<td>0.21</td>
<td>0.83</td>
</tr>
</tbody>
</table>

Variables that were highly correlated and therefore projected on the same PCA factor were grouped together in the analysis (indicated in **bold** font). WordFre = word form frequency; LemFre = lemma frequency; CNC = concreteness; IMG = imageability; N.Mean = number of meanings; N.Senses = number of senses; Action = action relatedness.

In order to simplify the EEG/MEG regression analysis, we grouped variables together according to the intercorrelation pattern, as in previous studies (Hauk, Davis, et al., 2008; Hauk, Davis, & Pulvermüller, 2008; Hauk, Davis, et al., 2006). Variables that showed high intercorrelation were subjected to a PCA, and only the first principal component was entered into the regression design. For example, bigram and trigram frequencies are highly correlated and likely to tap into similar orthographic processes. We therefore did not attempt to distinguish these two variables from each other and reduced them to one composite variable Bi/Trigram Frequency using PCA. Similarly, word form and lemma frequency were combined into one variable Frequency. Concreteness and imageability formed the variable Imageability, number of meanings and numbers of senses were grouped as Number of Meanings/Senses, and number of letters and number of orthographic neighbors resulted in Length/N. In the latter case, this led to a grouping of variables that are likely to reflect different processes, but the correlation between them was deemed too high to allow a clear separation of the two.

Table 2 shows the correlations between the original variables and the regressor from the PCA analysis. This demonstrates that the composite variables are indeed correlated with the original component variables and largely uncorrelated with other factors. Note that we used a multiple linear regression approach, which does not require predictor variables to be completely orthogonal.

**Procedure**

Each participant performed three standard psycholinguistic tasks: lexical decision (LexD), silent reading (SilR), and semantic decision (SemD). LexD required participants to distinguish between words and pseudowords, using the left hand middle finger for pseudowords and the left hand index finger for real words. SilR required participants to silently but attentively read words without making any overt response. SemD required participants to press a button using their left hand middle finger when they saw a target word corresponding to a person’s name. Task order was counterbalanced across participants.

For all three tasks, stimuli were presented for 100 msec (to focus attention and minimize eye movements), followed by a red fixation cross which had variable duration (\( M = 2400 \) msec, range = 2150–2650 msec). The average SOA was therefore 2.5 sec. Words were presented in a fixed width font (Courier New) in white on a black background. The longest words (seven letters) had a visual angle of \( 1.4^\circ \).

As LexD took twice as long as the other two tasks (because of the presence of pseudowords), it was split into halves so that the whole experiment contained four blocks of comparable length. Breaks of 10 sec were inserted after every minute of stimulus presentation. Each block lasted for 11 min except for SemD, which lasted 12 min because of the 20 additional target trials. Before the first block of LexD and SemD, a practice block with 10 items was provided to ensure both tasks were well understood.
As SiIR required no response inside the scanner, participants were administered a surprise postscan recognition memory test to ensure they had attended to the stimuli. In this test, they were presented 40 words one at a time and were required to indicate whether they had seen the words in the scanner or not by button press. Half of the words had been presented previously, and the other half were matched controls. Signal detection analyses were conducted to compute sensitivity ($d'$) from the difference between hits (correct responses to previously seen words) and false alarms (incorrect endorsing as old a previously unseen control word; cf. Snodgrass & Corwin, 1988). The same method was used to compute a $d'$ measure of name detection accuracy in SemD.

**Data Acquisition and Preprocessing**

MEG data were acquired using a 306-channel Neuromag Vectorview system, which contained 204 planar gradiometers and 102 magnetometers at MRC Cognition and Brain Sciences Unit. EEG data were acquired using a 70-electrode EEG cap (EasyCap, Falk Minnow Services, Germany). To ensure accurate coregistration with MRI data, the positions of five head position indicator coils attached to the EEG cap, three anatomical landmark points (bilateral preauricular points and nasion), and 60–100 additional points covering the whole scalp were digitized with a 3-Space Isotrak II System (Polhemus, VT). The EOG was recorded by placing electrodes above and below the left eye (vertical EOG) and at the outer canthi (horizontal EOG).

The signal-space separation method implemented in the Maxfilter software of Neuromag was applied to the raw MEG data to remove noise generated from sources distant to the sensor array (Taulu & Kajola, 2005). In this process, movement compensation was applied, bad MEG channels were interpolated, and data were down-sampled to a sampling interval of 4 msec. Data acquired in all blocks except the first one were interpolated to the sensory array of the first block. A band-pass filter between 0.1 and 40 Hz was applied using MNE software tools (Gramfort et al., 2014). For averaging, the raw data were divided into epochs of 600 msec, starting from 100 msec before stimulus onset. Epochs were rejected if maximum–minimum amplitudes in the −100 to 500 msec interval exceeded the following thresholds: 100 μV in the EEG, 100 μV in the EOG, 2500 fT in magnetometers, 1000 fT/cm for gradiometers. Raw data were browsed for each participant to check for consistently bad EEG channels, which were subsequently interpolated.

High-resolution structural T1-weighted MRI images were collected using a Siemens 3T Tim Trio MR system with a 12-channel head matrix coil at the MRC Cognition and Brain Sciences unit. They were acquired using a 3-D MPRAGE sequence, field of view 256 mm × 240 mm × 160 mm, matrix dimensions 256 × 240 × 160, 1 mm isotropic resolution, repetition time = 2250 msec, inversion time = 900 msec, echo time = 2.99 msec, flip angle = 9°.

**Parametric Analysis**

Multiple linear regression analysis was applied to our EEG and MEG data following the approach used for EEG and MEG data in previous studies (Miozzo et al., 2014; Hauk et al., 2009; Hauk, Davis, et al., 2006). All predictor variables were entered simultaneously into a linear model. This results into a set of linear estimators for each variable, which were applied across trials at each EEG/MEG sensor at each time point for each individual data set. The resulting event-related regression coefficients (ERRCs) for each predictor variable were then subjected to further analysis. Similar to the previous studies, we focused our analysis on five time windows around peak activations from root mean square curves for words in three tasks, as shown in Figure 1: 92–124 msec (in short “100 msec”), 144–176 msec (“160 msec”), 200–300 msec (“250 msec”), and 300–400 msec (“350 msec”).
ERRCs in sensor-based analyses can be interpreted similarly to “activation differences” between two types of word: A positive ERRC indicates that activation increases with increasing values of the variable and vice versa for negative ERRCs. However, ERRCs and ERP/ERF activation differences have the same ambiguity with respect to the direction of neural effects: A positive difference between items of Types A and B (i.e., A > B) does not reveal whether A is “more positive” or B is “more negative” without knowing whether A and/or B produce a positive or negative going response themselves. This problem also exists in source space, where activation values are “signed” with respect to whether the current flows out of or into the cortical surface. This sign is usually not of interest, and we are mainly interested in whether activity intensity (i.e., the absolute difference from zero) increases or decreases. We applied the following procedure to address this problem.

In the MNE source space, the sign of ERRCs was adjusted to indicate whether an increase in a variable value increases or decreases absolute brain activation. We exploited the fact that overall activity can be modeled as the average of all items (Avg), plus additional contributions from different predictor variables, for example, predictor \( P \). Computing the difference \( |\text{Avg} + P| - |\text{Avg}| \), where \(| |\) indicates the absolute value (i.e., removing the sign), at a particular vertex tells us whether the predictor \( P \) increases or decreases overall activity (depending on whether the result is positive or negative, respectively). This procedure was applied for every predictor variable at each vertex, and the resulting values were subjected to statistical analysis and display.

**Source Estimation**

Our source estimation procedure followed the standard procedure described for the MNE software (Gramfort et al., 2014). Minimum norm estimates (Hauk, 2004; Hämäläinen & Ilmoniemi, 1994) were computed on individually reconstructed cortical surfaces using boundary element models of the head geometry derived from each participant’s structural MRI images. EEG/MEG sensor configurations and MRI images were coregistered based on the matching of about 60–100 digitized additional points on the scalp surface with the reconstructed scalp surface from the FreeSurfer software (Version 4.3; surfer.nmr.mgh.harvard.edu/). Structural MRI images were processed using the automated segmentation algorithms of FreeSurfer (Dale, Fischl, & Sereno, 1999; Fischl, Sereno, & Dale, 1999). The noise covariance matrices for each data set were computed for baseline intervals of 200 msec duration before the onset of each stimulus. For regularization, the default signal-to-noise ratio in the MNE software was used (SNR = 3).

The result of the FreeSurfer segmentation was processed further using the MNE software package (Version 2.6). The original triangulated cortical surface (consisting of several hundred thousand vertices) was spatially down-sampled to a grid using the traditional method for cortical surface decimation with an average distance between vertices of 5 mm, which resulted in approximately 10,000 vertices. A three-layer BEM containing 5120 triangles were created from scalp, outer skull surface and inner skull surface, respectively. Dipole sources were assumed to be perpendicular to the cortical surface. The combination of EEG, gradiometer, and magnetometer data was achieved by prewhitening these data types with their corresponding noise covariance matrices, as is standard in this kind of analysis (Gramfort et al., 2014; Fuchs, Wagner, Kohler, & Wischmann, 1999). Simulation and empirical studies have demonstrated increased sensitivity for combined EEG and MEG data, especially for spatially extended sources (Goldenholz et al., 2009; Henson, Mouchlianitis, & Friston, 2009; Molins, Stufflebeam, Brown, & Hämäläinen, 2008).

Source estimates were computed for each participant, task, and ERRC, respectively (Hauk, Davis, et al., 2006). The individual results were morphed to the average cortical surface across all participants, and a grand average was computed. These grand averages were then displayed on the inflated average cortical surface. Activity values for ROIs (see below) were extracted using MNE software and functions from the MNE Matlab toolbox.

**ROI Analysis**

Following the example from an influential fMRI study on letter string processing (Vinckier et al., 2007), seven ROIs were selected from posterior to anterior left inferior temporal region of EEG/MEG source space, as shown in Figure 1. EEG/MEG source estimates not only have limited spatial resolution compared with fMRI localizations but may also be systematically biased (e.g., to locations closer to the sensors for classical minimum norm estimation; Hauk, Wakeman, & Henson, 2011; Lin et al., 2006; Fuchs et al., 1999). A direct translation of fMRI coordinates to our source space is therefore not recommended. Instead, we used a data-driven approach that adjusts the locations of ROIs on the basis of independent contrasts in our own data set.

We selected ROIs along the lateral ventral temporal lobe to take into account that minimum norm estimation prefers source locations closer to the sensors, rather in deeper brain areas. The ROIs were placed at locations where the contrast All Words against Baseline (averaged across tasks, and orthogonal to our predictor variables) produced activation at least once in our analysis epoch. This guarantees that our measurement configuration is indeed sensitive to activity from these regions, and they are not located in “blind spots” (such as radial sources for MEG). We computed approximate Talairach coordinates for our ROIs and compared them with coordinates for the VWFA in the literature (−42 −57 −12 according to Vinckier et al., 2007). This peak coordinate was closest...
RESULTS

Behavioral Results

Mean accuracy in LexD was 94% (SD = 5%). In SilR, the mean $d'$ of the postscan word recognition tests was 0.94 (SD = 0.14), which was significantly above 0 ($t(14) = 6.74$, $p < .001$; a score of zero indicating chance recognition). As participants were not warned about this memory test before the scanning session and different stimuli were used for each task, this result demonstrates that participants attended to the stimuli in SilR. Accuracy in SemD was high (99% correct, $SD = 1$%) and was also reflected in a high mean $d'$ of name detection in of 4.36 ($SD = 0.16$), which was significantly above 0 ($t(14) = 27$, $p < .001$). A multiple linear regression analysis of RTs to words in LexD yielded the results summarized in Table 3.

Of the variables that are relevant for the following EEG/MEG results, Frequency and Imageability were significantly negatively correlated with RTs. In addition, Action-relatedness showed a significant negative correlation.

General Time Course of Word Activation

As shown in Figure 1, the time course of signal-to-noise ratios for the combination of EEG and MEG sensors exhibited peaks at around 108, 160, and 250 msec after word onset. MNE source estimation revealed a spread of activation starting in bilateral posterior occipital cortex at around 100 msec, moving to anterior temporal lobes around 250 msec, with more activation in the left hemisphere. General activity decreased at later latencies. Task effects on the average response to written words have already been reported elsewhere (Chen et al., 2013). Here, we focus on task-induced changes in responses correlated with specific psycholinguistic predictor variables. These effects indicate that the information retrieved for written words differed depending on the task that participants perform.

Interestingly, responses did not show activation for words overall in left inferior frontal areas or around the angular gyrus. Note that we used combined EEG and MEG for source estimation, and so a lack of activity cannot be due to lack of sensitivity of either of these imaging methods in isolation. This pattern of activation justifies our focus on ROIs along the left ventral temporal lobe.

Table 3. Behavioral Regression Analysis in Lexical Decision Task

<table>
<thead>
<tr>
<th></th>
<th>EEG/MEG (n = 15)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length/N</td>
<td>0.0047</td>
</tr>
<tr>
<td>Bigram/trigram frequency</td>
<td>−0.0047</td>
</tr>
<tr>
<td>Word/lemma frequency</td>
<td>−0.1493 ***</td>
</tr>
<tr>
<td>Concreteness/imageability</td>
<td>−0.0932 **</td>
</tr>
<tr>
<td>Number of meanings/senses</td>
<td>0.0267</td>
</tr>
<tr>
<td>Action relatedness</td>
<td>−0.0485 **</td>
</tr>
</tbody>
</table>

Regression coefficients ($\beta$) for each regressor averaged across participants. Asterisks indicate whether a random effect analysis revealed that the regression efficient was significantly different from 0 across participants (*$p < .05$, **$p < .01$, ***$p < .001$).
Parametric Source Space Results

In the following, we will report the significant results from our ROI analyses, separately for each latency range. First, to validate our regression analysis in combination with source estimation, we present the source space result for the variable Length/N around 100 msec (Figure 2). At this latency, the effect can be assumed to be dominated by the word length (number of letters) component, which has been shown to produce larger amplitudes in posterior areas in several previous ERP and event-related field studies (Hauk et al., 2009; Hauk & Pulvermuller, 2004; Assadollahi & Pulvermuller, 2003). This pattern of results was confirmed in our data, which showed distinct peaks of positive correlation for Length/N in occipital brain areas. Combining activation across left and right occipital ROIs and all tasks produced a marginally significant difference from zero ($t(14) = 2.00, p = .068$) but reached significance in right occipital cortex ($t(14) = 2.2, p < .05$). We did not find task effects on Length/N at this latency. Note that Length/N was only entered into our analysis as a covariate, and the range of word lengths in our stimulus set may have been too small to produce more reliable results. Nevertheless, this analysis illustrates the sensitivity of our multiple regression analysis as well as the spatial resolution of our source estimation procedure.

The source distributions and ROI bar graphs that address our main objectives are shown in Figures 3 and 4.

Figure 2. Parametric source space result for the variable Length/N at 100 msec. The source distribution (in rear view) shows peaks of positive correlation in occipital cortex as expected. The bar graph presents results for an ROI analysis in left and right occipital cortex for activation averaged across tasks. Note that Length/N was entered into the analysis only as a covariate, but these results illustrate the sensitivity and validity of our multiple regression analysis in combination with source estimation.

Figure 3. Parametric source space results in left ventral temporal cortex for effects before 200 msec. The selection of latency ranges and ROIs corresponds to Figure 1. Bar graphs present ROI results for each task separately. Source distributions represent the task in which ERRCs most reliably differ from zero (LexD and SilR, respectively). The numbers below the bar graphs indicate individual ROIs, displayed as black lines in the brain images. ROI 3 was closest to the peak coordinate for VWFA as reported in Vinckier et al. (2007). Black rectangles indicate ROIs where the factor Task produced significant effects. Horizontal lines indicate significant differences between tasks within ROIs. Symbols on bars indicate ERRCs that differed from zero: *p < .1, *p < .05, **p < .01.
Our most important question is whether task effects occur already at earliest stages of lexico-semantic information retrieval. Previous studies have shown that these processes should begin before 200 msec (Hauk et al., 2012; Pulvermüller et al., 2009). We therefore present source space results for the early (pre-200 msec) latency ranges in Figure 3 and results for later latencies in Figure 4.

100 msec

In the earliest time window (92–124 msec), we found that effects of Bi/Trigram Frequency on neural responses were modulated by the task participants performed. The two-way repeated ANOVA (Region, Task) in source space revealed a significant Task × Region interaction ($F(12, 168) = 2.7, p < .01, \varepsilon = 1$). Post hoc one-way ANOVAs in each ROI revealed that task modulation of brain responses to Bi/Trigram Frequency was significant in a posterior fusiform region (ROI 2; $F(2, 28) = 3.6, p < .05, \varepsilon = 1$) and an anterior inferior temporal area (ROI 5; $F(2, 28) = 3.5, p < .05, \varepsilon = 0.9$). This interaction was due to a more positive correlation in LexD than SemD in the posterior ROI 2 ($t(14) = 2.7, p < .05$) and a more negative correlation in LexD than SilR in the anterior inferior temporal ROI 5 ($t(14) = 2.6, p < .05$). Within ROI 2, Bi/Trigram Frequency effects were significantly positive in LexD ($t(14) = 2.9, p < .05$) and marginally significantly negative in SemD ($t(14) = 1.8, p < .1$). Within ROI 5, Bi/Trigram Frequency effects were marginally significantly negative in LexD ($t(14) = 1.8, p < .1$).

160 msec

Our analyses in the time window 144–176 msec revealed effects of Frequency and Imageability, both of which were modulated by the factor Task. For Frequency, the two-way ANOVA with factors Task and Region revealed a significant Task × Region interaction ($F(18, 252) = 1.8, p < .05, \varepsilon = 0.8$). Effects of word frequency on behavioral responses are generally facilitatory, which would predict a negative correlation of Frequency with brain activation. Post hoc one-way ANOVAs revealed a significant effect of Task in ROI 4 only ($F(2, 28) = 4.6, p < .05, \varepsilon = 1$), because of a more negative correlation between frequency and activity during LexD than during SilR ($t(14) = 2.9, p < .05$) and SemD ($t(14) = 2.4, p < .05$). Note that ROI 4 is in the vicinity of the putative VWFA. Within ROI 4, frequency effects were significantly negative in LexD ($t(14) = 3.1, p < .01$).

Similarly, previously reported behavioral effects of imageability (if present) have usually been facilitatory (i.e., faster behavioral and reduced neural responses for more imageable words, hence a negative correlation between imageability and these measures). For our variable...
Imageability, the two-way repeated ANOVA (Task, Region) revealed a significant main effect of Task ($F(2, 28) = 3.5, p < .05, \epsilon = 1$) because of more negative correlation in LexD than SilR ($t(14) = 2.6, p < .05$). We performed one-way ANOVAs with factor Task in individual ROIs to substantiate the main effect across regions. A significant effect emerged in ROI 4 ($F(2, 28) = 3.7, p < .05, \epsilon = 1$) because of more positive correlation between Imageability and neural responses in SilR than LexD ($t(14) = 2.7, p < .05$). Within ROI 4, Imageability effects were significantly positive in SilR ($t(14) = 2.4, p < .05$). Thus, effects of Imageability were distributed across all ROIs but were most reliable in the vicinity of the putative VWFA.

**250 msec**

We observed task-independent effects of Frequency and Bi/Trigram Frequency in the latency range 200–300 msec.

For Frequency, planned one-sample $t$ tests showed that Region 5 was strongly positively correlated with Frequency across tasks ($t(14) = 5.0, p < .001, \text{Bonferroni-corrected}$), as shown in Figure 4. In the adjacent Region 6, there was a nonsignificant trend for a positive Frequency effect ($t(14) = 2.2, p < .05 \text{uncorrected}$). Although word frequency effects associated with facilitated word retrieval have usually been associated with negative correlations, positive frequency effects have been reported and interpreted in terms of semantic activation. In our data, this corresponds well to the localization of these effects into anterior temporal regions, which will be discussed below.

For Bi/Trigram Frequency, the two-way ANOVA (Task, Region) revealed a significant main effect of Region ($F(6, 84) = 3.30, p < .05, \epsilon = 0.8$). Post hoc paired $t$ tests for each pair of regions revealed significant differences between ROI 6 and each of ROIs 1, 2, 3, and 4 (all $p$s < .05). Furthermore, ROI 3 differed from ROIs 5 and 7 (both $p$ < .05). Overall, Bi/trigram Frequency showed more negative correlation in the anterior compared with posterior inferior temporal gyrus.

**350 msec**

The latency range 300–400 msec showed task-independent effects of Frequency.

For Frequency, the two-way ANOVA (Task, Region) revealed a significant main effect of Region ($F(9, 126) = 2.6, p < .05, \epsilon = 0.6$), because of larger positive Frequency effects in anterior compared to posterior inferior temporal gyrus: ROIs 6 and 7 showed stronger effects than ROI 2 or 4; ROI 3 differed from ROI 6 ($p < .05$), but not from ROI 7. No main effects of Task or Region and Task interaction were found in this time window ($F < 0.9, p > .5$).

Planned one-sample $t$ tests revealed a significant positive correlation with Frequency across tasks in Region 6 ($t(14) = 3.6, p = .003, \text{Bonferroni-corrected}: .005$). In the adjacent Region 7, there was also a nonsignificant trend for a positive Frequency effect ($t(14) = 2.2, p < .05 \text{uncorrected}$).

**DISCUSSION**

Task modulation in occipitotemporal cortex occurred for the lexical predictor variable Frequency and the semantic predictor Imageability around 160 msec, preceded by orthographic effects of the variable Bi/Trigram Frequency around 100 msec. The finding that the distribution of early brain activity for specific psycholinguistic variables depends on task demands indicates that top–down modulation already affects early information retrieval processes in visual word recognition. Some previous studies have already argued for flexible lexical processing based on behavioral data (Balota & Yap, 2006) and attentional sensitization based on masked priming N400 effects (Kiefer & Martens, 2010). We here present evidence for task modulation of early neural responses contributing to single-word processing from spatiotemporal brain activation patterns derived from combined EEG/MEG measurements.

Although the general pattern of results with respect to our subtle manipulations of tasks and stimulus variables is complex, we could replicate previous findings with respect to the neural time course of visual word recognition seen previously using single tasks. Recent studies from different groups converge on the view that lexicosemantic information retrieval can begin, but may not be complete, around 160 msec (Amsel et al., 2013; Hauk et al., 2012). This view is supported by effects of Frequency and Imageability on neural responses observed at around 160 msec in our study. We can also confirm previous evidence for a fast cascade of effects for different psycholinguistic variables within the first 250 msec after word presentation (Hauk, Davis, et al., 2006), highlighting the necessity to track brain activity with high temporal resolution.

We used three psycholinguistic tasks that all explicitly required our participants to focus their attention on linguistic aspects of the stimuli. They differed with respect to response selection demands, using a task manipulation similar to previous behavioral studies (Balota et al., 2004; Balota & Chumbley, 1984). Importantly, it is unlikely that differences with respect to late response selection and execution leads to the specific effects observed at early latencies. We did not observe task effects on average word activation at the latency of the P1 component, which is evidence that our tasks were similar with respect to visual attention demands (Figure 1, Chen et al., 2013).

A lot of neuroimaging research has been dedicated to determine the role of the putative VWFA in ventral occipitotemporal cortex (Dehaene & Cohen, 2011; Price & Devlin,
term memory (Norris & Kinoshita, 2012; Norris, 2006). For a task like lexical decision in which words are presented in isolation, word frequency is a near-optimal prior. Our results indicate that an integration of information from the perceptual input and long-term memory occurs around the VWFA.

Imageability effects were distributed across several ROIs around 160 msec, with larger positive regression coefficients in silent reading compared to lexical decision. The most reliable effect occurred in the same ROI as the word frequency effect, indicating that activity in this area is affected by both lexical and semantic information. Positive correlations for imageability in ventral temporal cortex have been reported by several previous fMRI studies (Sabsevitz et al., 2005; Fiebach & Friederici, 2004; Wise et al., 2000), but some failed to find such effects (Binder, Westbury, McKiernan, Possing, & Medler, 2005; Jessen et al., 2000). One study also reported an imageability effect using a silent reading task (Hauk, Davis, Kherif, et al., 2008). This task resembles natural reading, so far as we usually read for meaning and not to perform a categorical decision. It may surprise that we did not find more reliable effects in our semantic decision task. However, our semantic task required participants to decide whether a letter string was a person’s name or not. This task does not encourage the retrieval of concrete semantic features, for example, related to our senses or actions, but it did affect anterior temporal lobe regions in our previous analysis (Chen et al., 2013). The effects of different semantic tasks on spatiotemporal brain dynamics should be investigated in future research.

In addition to the early task modulations, it is also striking that we found task-independent effects of Bi/Trigram Frequency and Frequency after 200 msec in anterior temporal areas. Bi/Trigram Frequency correlated negatively with activation, similar to previous ERP results (Hauk, Davis, et al., 2006; Hauk, Patterson, et al., 2006). Interestingly, the task-independent correlation with Frequency between 200 and 300 msec was positive and persisted in the 300–400 msec time window. In previous fMRI studies, positive correlations with word frequency have been associated with semantic processing, because higher-frequency words might be “more likely to elicit automatic activation in a semantic network due to their extensive exposure” (Graves, Desai, Humphries, Seidenberg, & Binder, 2010; see also Carreiras, Riba, Vergara, Heldmann, & Munte, 2009). This corresponds well with our effect in the anterior temporal lobes, which have been assigned the role of a semantic hub—linking word forms with distributed semantic networks—based on neuropsychological and neuroimaging evidence (Patterson et al., 2007). The absence of task effects at later latencies in the ventral stream does not preclude the possibility that they may exist in other brain regions, but this was beyond the scope of this article.

The shift of activation from posterior to anterior areas over time and the absence of task effects in temporal lobe ROIs at later latencies suggest that the end point
of the word recognition process in each task was the retrieval of meaning—all routes lead to semantics. This conforms to the fact that in most real-life situations we process letter strings to retrieve meaning, and it confirms established behavioral evidence that word meaning can contribute to performance in tasks that do not require semantic information (Woolfams, 2005; Chumbley & Balota, 1984). However, this does not imply that earlier processes are not modulated by task demands, as we could show in our data.

What is the functional significance of our observed top–down effects on early brain responses? The essential computation underlying word recognition is the optimal combination of perceptual evidence with prior knowledge from long-term memory (Norris, 2006, 2013). What is “optimal” depends on the goal of the person reading, the material being read, and (in the context of traditional psychological tasks) the decision to be made at that time. Efficient recruitment of neuronal resources at early stages of processing should therefore take into account the final goal of the recognition process. It may not make sense to ask questions about “word recognition” without also asking “word recognition for what?” This implies that it does not make sense to separate word recognition into a “retrieval” and a “decision” stage—the two are strongly intertwined. Surprisingly few neuroscientific studies have investigated task effects on word recognition, and more research should be dedicated to this issue in the future.

It is important to note that, although our findings support top–down modulation of early brain responses, this does not necessarily imply recurrent activation or feedback mechanisms during reading. On the one hand, the speed and efficiency of visual object recognition have been taken as evidence for fast feedforward sweeps along the ventral stream (Serre, Oliva, & Poggio, 2007; Riesenhuber & Poggio, 2002; Lamme & Roelfsema, 2000; Thorpe, Fize, & Marlot, 1996). On the other hand, interactive levels of processing have been part of models of word recognition for a long time (Rogers et al., 2004; McClelland & Rogers, 2003) and have been suggested as a general principle of stimulus recognition in the framework of predictive coding (Bastos et al., 2012; de-Wit, Machisen, & Putzeys, 2010). Our results are, in fact, consistent with both views. Task demands may change the parameters of a feedforward stream and hence need not imply interactive processing (Norris, McQueen, & Cutler, 2000). This does not require higher-level areas to reactivate or modulate activation in lower-level areas during stimulus processing. Determining the neuronal mechanisms by which top–down modulation is achieved will require detailed connectivity analyses of spatiotemporal brain dynamics. Our present results are an important step in this direction.

In conclusion, our results lift the “curse of automaticity” (Balota & Yap, 2006) by demonstrating that the topography of the earliest brain responses sensitive to word-specific processes can be modulated by task demands. Thus, even a highly overlearned process such as word recognition should be considered as flexible rather than automatic.

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REFERENCES


