

The Journal of Neuroscience

<http://jneurosci.msubmit.net>

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Commercial Interest:

**Uncovering the hidden layer of semantics:
Spatio-temporal dynamics of lexico-semantic processing in the anterior temporal
lobe**

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Abbreviated title: Uncovering the hidden layer of semantics

Number of Pages/Figures/Tables: 27/4/3

Number of Words: Abstract: 247, Introduction: 528, Discussion: 1383

Abstract (247 words)

How do people so rapidly and effortlessly understand that the words “yummy” and “delicious” refer to the same concept despite their very different written forms? One view, initiated by research on semantic dementia and supported by results of some functional brain imaging studies of healthy participants, is that this comprehension and generalization requires an amodal semantic hub, located in the anterior temporal lobes (ATL) and corresponding to a hidden layer in a connectionist network. Essential properties of such a hub region are that it should be modulated by lexico-semantic variables at the earliest stages of word recognition. Here, we tested these properties using combined EEG and MEG measurements and distributed source estimation. Letter strings were presented in two different tasks: lexical decision (LexD) and semantic decision (SemD). In LexD, stimuli were orthogonally varied over lexicality (words vs. nonwords) and orthographic typicality (typical vs. atypical), and were presented in two foil contexts varying in difficulty (pseudoword vs. pseudohomophone). The SemD task required concreteness judgments, and allowed us to test the sensitivity of ATL to a specific semantic variable. In LexD, effects of lexicality and task context involving left ATL emerged around 240 ms, following earlier effects of orthographic typicality around 100 and 180 ms. In SemD, a concreteness effect was observed in left ATL also around 240 ms. We propose that these effects at around 240 ms may reflect the processes performed by a hidden layer in a connectionist network, linking word form inputs to distributed semantic networks.

Significance statement (119 words)

Connectionist computational modelling has proposed that conceptual categorization and generalization require a “hidden” level of representation that functions as an amodal semantic hub. Imaging has implicated a network of regions in semantic processing, and neuropsychological evidence has localized the amodal hub to the anterior temporal lobe. If the ATL does act as a hub, it should become active very early in processing, yet there has been no direct assessment of this hypothesis to date. Here we tested this prediction using combined EEG/MEG to track brain activation during word recognition and comprehension. The anterior temporal lobe showed sensitivity to spelling typicality at 100ms after stimulus presentation, and to word-likeness and word meaning at 240ms, consistent with the amodal hub hypothesis.

Introduction (528 words)

Healthy people easily recognize and comprehend the words and objects constantly confronting them. The notion that semantic information, at least referring to perceptual and action concepts, is partly represented in distributed brain networks comprising sensorimotor cortices has received substantial support from functional neuroimaging research (Martin, 2007; Pulvermüller, 2005). It nevertheless remains unclear precisely how, where and when this distributed information is bound together in order to allow discrimination, generalization and categorization. Most existing evidence stems from neuropsychology and metabolic neuroimaging methods. Here, we tested essential properties of a semantic hub in spatio-temporal data using combined electro- and magnetoencephalography (EEG and MEG).

Some authors have argued that such abilities across multiple different input modalities require an amodal “semantic hub”, which connects inputs with distributed semantic brain networks (Lambon Ralph, 2014; Patterson, Nestor, & Rogers, 2007), and corresponds to a hidden layer in a connectionist network that maps between multiple modalities (Plaut, 2002; Rogers, Lambon Ralph, Hodges, & Patterson, 2004). A proposal that the anterior temporal lobes (ATL) might represent such a hub has arisen from research on semantic dementia, a neurodegenerative condition in which ATL atrophy produces a selective impairment of semantic knowledge (Patterson, et al., 2006). One characteristic of this impairment is a stronger deficit in recognizing objects or words that are atypical for their category than those that are typical (e.g., a camel vs. a horse) (Rogers, Lambon Ralph, Hodges, et al., 2004; Woollams, Cooper-Pye, Hodges, & Patterson, 2008). Furthermore, neuroimaging studies have shown increased ATL

activation for tasks or stimuli that load heavily on semantic knowledge (Visser, Jefferies, & Lambon Ralph, 2010; Woollams, Silani, Okada, Patterson, & Price, 2011).

The proposal of an amodal semantic hub as well as its localization to the ATL is still controversial. An early proposal was that conceptual knowledge is subserved by multiple convergence zones which are themselves distributed across temporal, parietal and frontal lobes (Damasio, 1989; Meyer & Damasio, 2009). Binder and colleagues (Binder & Desai, 2011), for example, localized this kind of semantic function to medial temporal lobe structures for objects, to the angular gyrus for event information and language, and to the ATL for affective and social processing.

Here we advance this debate by testing for an essential feature of a semantic hub: if an area serves as a hub to allow access from word form to a distributed network representing aspects of its meaning, then it should become active at the earliest stage of processing. We also probed the role of this area in written word recognition using a lexical decision (LexD) task in which the degree of semantic involvement was manipulated by presenting words that varied in the orthographic typicality of their spellings (see Hauk et al., 2006) and nonwords that varied in their similarity to words (see Woollams et al., 2011). We then used a semantic decision (SemD) task requiring a concreteness judgement (see Dhond et al., 2007) to test the ATL's sensitivity to a specifically semantic variable. On the hypothesis that the ATL serves as a semantic hub, we would expect this region to show activation at around 200 ms in both tasks (Amsel, Urbach, & Kutas, 2013; Hauk, Coutout, Holden, & Chen, 2012).

Methods

Participants

17 participants (12 female) entered the EEG/MEG analysis after three subjects were excluded due to excessive movement, eye blinking artifacts or measurement error. A reduced version of the Oldfield handedness inventory (Oldfield, 1971) yielded a laterality Quotient of 82 (SD=23). The average age of our participants was 27 (SD=6). All participants were native English speakers, had normal or corrected-to-normal vision and reported no neurological disorder or dyslexia. They were paid 10 pounds per hour for their participation (a minimum of £20 for the whole experiment). The experiment was approved by the Cambridge Psychology Research Ethics Committee.

Stimuli

In the lexical decision task, the stimulus set consisted of 96 monomorphemic content words and 96 nonwords, which have already been used and described in a previous study (Woollams, et al., 2011). Stimuli were subcategorized as orthographically typical (e.g. “tiger”) or atypical (e.g. “rhyme”), as determined by their positional bigram frequency in the McWord on-line database (Medler & Binder, 2005), which computes values based on the CELEX psycholinguistic database (Baayen, Piepenbrock, & van Rijn, 1993). Furthermore, words were presented in either a pseudohomophone (PH) context, where each foil was phonologically identical to one of the target words (e.g. “train/trane”, “nymph/nimpf”), or a pseudoword (PW) context, where the foils were orthographically similar but not phonologically identical to the stimulus words (e.g. “tiger/tager”, “rhyme/rhyke”). As in the examples, words and nonwords were paired, such that each word had an orthographically similar nonword partner, although these were never

presented in the same block. Whether the word or nonword of a pair appeared first was counterbalanced across participants.

These stimulus categories were matched with respect to a range of psycholinguistic variables (see Table 1). All eight conditions were matched on number of letters and syllables. They did not differ significantly in terms of word frequency, and the nonwords were comparable in terms of number of letters changed from the baseword. Between-item Lexicality by Typicality by Context ANOVAs confirmed only a main effect of orthographic typicality for the type and token measures of letter and bigram frequency (Woollams, et al., 2011). For the type and token trigram and orthographic neighbourhood measures, there were significant effects of orthographic typicality, with marginally significant effects of lexicality indicating that the nonwords actually tended to be more word-like than the words on these measures (see (Woollams, et al., 2011) for further details).

In the semantic decision task, participants were presented with 184 monomorphemic words, 92 abstract and 92 concrete, matched for a number of psycholinguistic variables (Table 2). Independent sample t-tests indicated that concrete and abstract word sets differed on concreteness and imageability ($t>19.36$, $p<.0005$), but did not differ significantly on Kucera-Francis or CELEX frequency, rated familiarity or number of letters/phonemes/syllables.

Procedure

In both LexD and SemD tasks, stimuli were presented for a duration of 150 ms, with an average SOA of 2400 ms jittered between 2150 and 2650 ms). They appeared as white on black in 28-point Arial font within a visual angle of 4 degrees in a slightly dimmed and acoustically shielded MEG chamber. Participants responded by button press with the right hand, using index and middle finger to distinguish between real words and pseudowords and concrete and abstract words, respectively. Breaks were included after about every 50 trials. Participants had a few minutes of practice before the experiment until they felt comfortable with the task. The first two trials after each break and at the beginning of each block were not included in the analysis.

Pseudohomophone and pseudoword contexts were presented in different blocks the order of which were counterbalanced across participants. Participants were not explicitly instructed about the context manipulation. LexD was always run before SemD, with another lexical decision task intervening between them, the results of which will not be considered here. There was no overlap between stimuli used in any of the tasks.

EEG/MEG data acquisition and pre-processing

MEG data were acquired at the MRC Cognition and Brain Sciences Unit, Cambridge, UK, using a 306-channel Neuromag Vectorview system (Elekta AB, Stockholm, Sweden), which contained 204 planar gradiometers and 102 magnetometers. EEG data were acquired simultaneously using a 70-electrode EEG cap (EasyCap GmbH, Herrsching, Germany), with the recording reference electrode attached to the nose, and the ground electrode to the left cheek. The electrooculogram (EOG) was recorded by placing electrodes above and below the left eye (vertical EOG) and at the outer canthi

(horizontal EOG). Data were acquired with a sampling rate of 1000 Hz and a band pass filter 0.03 to 330 Hz.

To ensure accurate co-registration with MRI data, the positions of 5 Head Position Indicator (HPI) coils attached to the EEG cap, 3 anatomical landmark points (bilateral preauricular points and nasion), and 50-100 additional points covering the whole scalp were digitized with a 3Space Isotrak II System (Polhemus, Colchester, Vermont, USA).

The signal-space separation (SSS) method implemented in the Maxfilter software (Version 2.0) of Elekta 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 downsampled to a sample interval of 4 ms. For each participant, data acquired in all blocks except the first one were interpolated to the sensory array of the first block using the SSS method in Maxfilter software, in order to correct for movements between blocks.

Data were off-line band-pass-filtered between 0.1 and 30 Hz using MNE software (Version 2.6, <http://martinos.org/mne/stable/index.html>). They were then divided into epochs of 600 ms, starting from 100 ms before stimuli onset. Epochs were rejected if maximum-minimum amplitudes in the -100 to 500 ms interval exceeded the following thresholds: 100 μ V in the EEG, 100 μ V in the EOG, 2500 fT in magnetometers, 1000 fT/cm for gradiometers. Only trials with correct responses were included in the averaging procedure. Raw data were inspected for each subject to check for consistently bad EEG channels, which were subsequently excluded from analysis.

EEG/MEG sensor space analysis

In order to describe the quality of our data and to determine latency ranges of interest, we displayed the RMS of the signal-to-noise ratio (SNR) across all magnetometers, gradiometers and electrodes. The computation of SNRs prior to RMS transformation renders the values for all channels unit-less (original measurements are in T,T/m and μ V, respectively), and allows the computation of a combined measure for display.

Source estimation and statistical analysis

Our source estimation procedure followed the standard procedure described for the MNE software (Gramfort, et al., 2014). Minimum norm estimates (Hämäläinen & Ilmoniemi, 1994; Hauk, 2004) were computed on individually reconstructed cortical surfaces using boundary element models of the head geometry derived from structural MRI images for each participant. EEG/MEG sensor configurations and MRI images were co-registered based on the matching of about 50-100 digitized additional points on the scalp surface with the reconstructed scalp surface from the FreeSurfer software (Version 4.3; <http://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 ms duration before the onset of each stimulus presented during the whole experiment. 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 downsampled to a grid using the traditional

method for cortical surface decimation with an average distance between vertices of 5 mm, which resulted in approximately 10000 vertices. For MEG, a boundary element model (BEM) containing 5120 triangles was created from the inner skull surface using a watershed algorithm. For EEG, a three-layer BEM containing 5120 triangles was created from scalp, outer skull surface and inner skull surface respectively. Dipolar sources were assumed to be perpendicular to the cortical surface. Source estimates were computed for each subject. The individual results were morphed to the average brain across all subjects, and a grand-average was computed. These grand-averages were then displayed on the inflated average cortical surface.

Our source analysis targeted the activation flow along the left temporal lobe, because of convincing evidence that processing of written words—even more than spoken words—is strongly lateralised to the left hemisphere (Marinkovic et al., 2003). Taking into account the spatial resolution limits of combined EEG/MEG measurements (Hauk, Wakeman, & Henson, 2011), we targeted three separate sections in the temporal lobe (posterior, middle, anterior). We defined regions-of-interest (ROIs) around peaks in the whole-brain activation maps for the evoked signals averaged across all stimuli. These maps revealed three prominent activation peaks in ventral occipital-temporal (vOT), inferior temporal (IT) cortex and anterior temporal lobe (ATL). The borders of ROIs were defined as approximately following the line of half-maximum amplitude of the corresponding peak, and were created in the MNE software. The average source amplitudes across vertices within these ROIs were computed for each condition and participant, and subjected to repeated-measures ANOVAs. Greenhouse-Geisser correction for degrees of freedom was applied where appropriate.

Results

Behavioral results

Mean reaction times and errors rates in the various experimental conditions, for the 17 participants included in the EEG/MEG analyses, can be seen in Table 3.

Lexical decision

A repeated measures ANOVA on reaction times with lexicality (nonwords/words), orthographic typicality (atypical/typical) and task context (pseudowords/pseudohomophones) as factors revealed longer reaction times to nonwords than words ($F(1, 16)=5.43, p=.033$) and to orthographically typical than atypical items ($F(1, 16)=5.02, p=.040$), with a trend for longer RTs in the pseudohomophone context ($F(1, 16)=3.73, p=.071$). The orthographic typicality effect for both words and nonwords was larger in the pseudohomophone context than the pseudoword context, as indicated by a significant Typicality by Context interaction ($F(1, 16)=9.09, p=.008$). The orthographic typicality effects were reliable for both words and foils in the pseudohomophone context ($t_{(16)}=2.74, ps<.015$), but for neither words nor foils in the pseudoword context ($t_{(16)}<.786, ps>.444$).

Parallel analyses of error rates revealed less accurate performance for nonwords than words ($F(1, 16)=5.43, p=.033$), to orthographically typical than atypical items ($F(1, 16)=5.02, p=.040$) and in the pseudohomophone than pseudoword context ($F(1, 10)=32.44, p<.0005$). There were significant interactions between orthographic typicality and foil context ($F(1,16)=17.50, p=.001$) indicating that, as per the reaction time analysis,

there was a stronger impact of typicality on performance in the pseudohomophone context ($ts(16)>1.99$, $ps<.064$) than the pseudoword context ($ts(16)<1.33$, $ps>.203$). There was also an interaction between lexicality and foil context ($F(1,16)=14.83$, $p=.001$), due to a much larger accuracy advantage for targets relative to foils in the pseudohomophone context ($ts(16)>2.18$, $ps<.050$) than the pseudoword context ($ts(16)<1.10$, $ps>.290$), consistent with the idea that pseudohomophones were indeed more word-like and hence more difficult to reject.

Semantic decision

For the semantic decision task, paired t-tests showed that reaction times were significantly longer for abstract words (mean=883ms; SD=119ms) than for concrete words (mean=783ms; SD=115ms) ($t(16)=6.23$, $p<.0005$). Similarly, error rates (ERs) to abstract words (mean=8.06%; SD=5.01%) were significantly higher than for concrete words (mean=4.48%; SD=4.30%) ($t(16)=2.45$, $p=.026$). Note that our 17 participants were faster and more accurate on average than the 10 participants in the study of Dhond et al. (2007) (RTs for abstract/concrete: 1164/1045 ms, ERs: 76/96 %).

EEG/MEG Results

Figure 1 about here

In order to illustrate the overall time course of brain activation, and to provide a measure of data quality in signal space, we present the root-mean-square (RMS) of

signal-to-noise ratio (SNR) across all recording channels in Figure 1A, for LexD and SemD separately. The first peaks in these curves occurred at 96 ms (for both LexD and SemD), 138 ms (LexD and SemD), 240 (LexD) and 244 (SemD) ms, as well as at 354 (LexD) and 348 (SemD) ms. This indicates that the general time course of activation was very similar for the two tasks. The first two peaks in the present study are slightly earlier than the corresponding peaks in our previous ERP study (Hauk, Patterson, et al., 2006). In order to avoid overlap of adjacent time windows, while still capturing the main dynamics from Figure 1A, we defined the following latency ranges for further analysis: 90-110 ms (referred to in the following as “100 ms”), 160-200 ms (“180 ms”), 220-260 ms (“240 ms”), and 320-360 ms (“340 ms”). We tested all latency ranges for LexD, which contained orthographic and lexical variables. For those latency ranges that showed effects of lexicality or foil context, we then tested whether ATL was sensitive to concreteness in SemD. We present whole-brain activation distributions for several latency ranges as well as activation time courses for ROIs in Figures 2 and 4.

ROI analysis in source space

In the following, we will report all significant effects of our ANOVAs on ROI activations in source space. Our main hypotheses concerned activation flow along the left temporal lobe, which was sub-divided into three sections and represented by a factor ROI in our ANOVA design. We will first present results for the LexD task, followed by the SemD task. Finally we will present results for a left inferior parietal ROI separately.

Difference distributions for variables of interest are presented in Figure 2 (LexD) and Figure 4 (SemD), respectively. The corresponding ROI statistics are summarized as bar graphs in Figure 3 and 4B, respectively. Whole-brain activation averaged across all

stimuli in LexD is displayed in Figure 1B. The activation maps for SemD are very similar and are not displayed. Both show a spread of activation from occipital areas around 100 ms to anterior temporal areas around 240 ms. Activations in inferior parietal and inferior frontal regions are weaker compared to those in temporal lobe, and do not exhibit clear peaks.

Lexical Decision

Figure 2 about here

100 ms

A main effect of Typicality across all ROIs occurred between 90-110 ms, with stronger activation for letter strings with atypical compared to those with typical orthography ($F(1,16)=5.49$, $p<0.05$, $\epsilon=0.64$), comparable with previous ERP studies (Hauk, Davis, Ford, Pulvermuller, & Marslen-Wilson, 2006; Hauk, Patterson, et al., 2006).

180 ms

An interaction of Typicality*ROI was found between 160-200 ms ($F(2,32)=4.41$, $p<0.05$, $\epsilon=0.767$). The main effect of Typicality approached significance (Atyp > Typ, $F(1,16)=3.95$, $p=0.064$). The Typicality effect was significant in ITC (Atyp > Typ,

$t=3.20$, $p<0.01$), and approached significance in vOTC (Atyp > Typ, $t=1.84$, $p=0.07$), but was non-significant in ATL ($t=-0.37$, $p>0.7$).

240 ms

An interaction of Typicality*ROI was found between 220-260 ms ($F(2,32)=9.23$, $p<0.01$, $\epsilon=0.767$). Atypical items produced more activation than typical items in ITC ($t=2.52$, $p<0.05$). This difference was not significant in ATL or vOTC ($t=-0.57$ and $t=0.44$, respectively, $p>0.5$).

The factor of Context interacted with ROI ($F(2,32)=3.78$, $p<0.05$ $\epsilon=0.98$). This effect was significant in vOTC (PH>PW, $t=-2.11$, $p<0.05$) and ATL (PW>PH, $t=2.16$, $p<0.05$), but not ITC ($t=0.84$, $p>0.4$). We also found an interaction between Context and Lexicality across ROIs ($F(1,16)=4.54$, $p<0.05$). Words produced more activation than nonwords in the PW context ($t=2.01$, $p<0.05$), but the difference was not significant in the PH context ($t=-1.06$, $p>0.29$).

340 ms

The main effect of Context was significant between 320-360 ms ($F(1,16)=7.97$, $p<0.05$), as was the interaction of ROI-by-Context ($F(2,32)=4.50$, $p<0.05$, $\epsilon=0.96$). Stimuli in pseudoword context produced more activation than in pseudohomophone context in ATL ($p<0.001$), and this was not significant in vOTC or ITC ($p>0.2$). The 4-way interaction ROI-by-Context-by-Lexicality-by-Typicality only approached significance ($F(2,32)=3.19$, $p=0.062$, $\epsilon=0.88$).

Semantic Decision

Figure 3 about here

Our previous analyses revealed that ATL activation is modulated by lexicality and task context around 240 ms. Although it has been argued that lexicality judgments involve semantics (Balota, Cortese, Sergent-Marshall, Spieler, & Yap, 2004; Chumbley & Balota, 1984; Evans, Lambon Ralph, & Woollams, 2012; Pexman, Hargreaves, Siakaluk, Bodner, & Pope, 2008; Rogers, Lambon Ralph, Garrard, et al., 2004), this of course does not prove that the effects at 240 ms in the ATL reflect semantic processing. A previous MEG study of concreteness decision reported higher activation for concrete than abstract words in left ATL at around 400ms and a reversal of this effect around 700ms, at which point a reversed effect was also apparent in the right ATL (Dhond et al. did not apply group statistics to their data, but instead based their inferences on signal-to-noise ratios in a dSPM analysis). We therefore considered the concreteness effects in semantic decision in the left and right ATLs in our two later time windows for comparison both to our lexical decision data and also previous concreteness judgement data.

240 ms

We found a marginally significant main effect of Concreteness, with concrete words producing more activation than abstract words ($F(1,16)=3.80$, $p=0.069$). We also found a main effect Hemisphere ($F(1,16)=5.32$, $p<0.05$: more activation in the left compared to the right hemisphere). We obtained a marginally significant interaction of

Hemisphere-by-Concreteness ($F(1,16)=3.40$, $p=0.084$): the Concreteness effect was significant in the left hemisphere ($F(1,16)=8.37$, $p<0.05$), but not in the right ($F(1,16)=0.061$, $p>0.8$). The direction of these effects was expected on the basis of Dhond et al's (2007) previous study.

340 ms

There was no significant Concreteness effect in the left hemisphere in this later phase ($F(1,16)=1.29$, $p>0.27$), but the main effect of Concreteness across hemispheres approached significance ($F(1,16)=4.12$, $p=0.059$: more activation for abstract compared to concrete words. However, the interaction of Hemisphere-by-Concreteness was not significant ($F(1,16)=2.55$, $p=0.13$). For comparison with Dhond et al. (2007), we still tested both hemispheres separately, which only revealed an effect in right ATL, with more activation for abstract than concrete words ($F(1,16)=4.72$, $p<0.05$).

Figure 4 about here

ROI analyses in inferior parietal lobe

Another brain area outside the temporal lobes that has been implicated in early semantic processing is the left angular gyrus (Binder & Desai, 2011; Binder, Desai, Graves, & Conant, 2009). We tested this area separately for effects in all the above latency ranges and in both tasks despite the fact that none of the whole brain distributions in Figures 1-3 suggested any activity in this area at a level comparable to the significant

effects reported above. In line with this, none of our tests yielded significant results in the inferior parietal ROI.

Discussion (1383 words)

This study explored the hypothesis that our ability to rapidly understand the meaning of written words depends upon activation of a semantic hub in the anterior temporal lobes which provides a gateway to more neurally distributed aspects of meaning. According to this view, we should see very early activation of the ATL in word recognition that resembles that seen in word comprehension. We therefore studied the effects of orthographic, lexical and semantic variables on spatio-temporal brain responses using combined EEG/MEG in a lexical and semantic decision task, respectively. The time course of brain responses was very similar across the two tasks, but we found specific differences with respect to our stimulus and task manipulations along the temporal lobe. Early effects of orthographic typicality occurred around 100 ms, followed by effects of lexicality, concreteness and foil context in the ATL at 240 ms. These results are consistent with models proposing that the ATL functions as an integrative hidden layer mediating between more modality specific inputs and outputs (Rogers et al., 2004a). Our data move beyond previous work using neuropsychology or metabolic neuroimaging by providing unique information concerning the time course of activation during written word recognition.

In our LexD task, we observed an early (~100ms) main effect of Typicality across ROIs, i.e. in ventral-occipital, mid-inferior temporal and anterior temporal lobe with higher activation for strings containing atypical letter combinations. This may seem surprising, since this type of orthographic effect at early latencies has previously been associated with posterior (occipito-)temporal cortex (Hauk, Patterson, et al., 2006; Woollams, et al., 2011). It is however well-established that even simple stimuli such as tone-clicks or visual flashes rapidly activate large brain networks, including frontal cortex (Bullier, 2001). We propose that a word stimulus activates, possibly “pre-sensitizes”,

ventral temporal cortex early-on. Letter strings with atypical orthographic patterns may require more resources to process initially, thus leading to larger activation across the whole ventral stream. At 180 and 240 ms, there was a significant effect of Typicality in the same direction only in mid-temporal cortex, a region supposed to be specialized (although not necessarily exclusively) for higher-level orthographic processing (Dehaene & Cohen, 2011; Price & Devlin, 2011).

At 240 ms only did effects of lexicality and task context emerge, involving the ATL, consistent with the view that word processing advances in a cascaded manner from orthography to semantics within about 250 ms (Hauk, Davis, et al., 2006; Pulvermuller, Shtyrov, & Hauk, 2009). There was more activation in the pseudoword than pseudohomophone context around 240 ms, and this effect was still significant in the 340 ms range. While it might seem that it is the pseudohomophone stimuli that should activate semantics more than pseudowords, this depends upon how semantic activation is used in the service of the task. Within some connectionist models (Harm & Seidenberg, 2004), lexical decision is made on the basis of comparing the external orthographic input to an internal orthographic representation generated from semantic activation. The internal representation will be more rapidly generated for pseudohomophones, and a mismatch with the external input detected. The internal representation for a pseudoword will take longer to generate, hence semantic processing for these items will continue for longer, resulting in higher activation in the ATL. This interpretation is also consistent with the higher activation for pseudohomophones than pseudowords in vOTC in the same time window, given the association of this area with orthographic processing.

We also found an interaction between foil context and lexicality at 240 ms in all temporal lobe areas including the ATL. There was higher activation for words than pseudowords, but not for words than pseudohomophones. This result is consistent with

connectionist accounts of lexical decision which invoke semantic stress as a decision metric, since pseudohomophones are designed to be more wordlike than pseudowords. In such a model, Plaut (1997) found that nonwords generate lower stress values than words over units in the semantic layer (higher stress is seen for words as these drive units to their extreme values most rapidly). This is consistent with the overall lexicality effect seen here, where words produce higher activation than nonwords. At the same time, Plaut (1997) found that pseudohomophones generated significantly higher stress values than pseudowords – in essence, the pseudohomophones were more wordlike in terms of the semantic activation they generated. This is consistent with the present finding that a significant lexicality effect was limited to the pseudoword context, and did not reach significance for the pseudohomophone context.

The interpretation of ATL activation in the lexical decision task as indexing semantic processing is further supported by results from the SemD task, where we observed more activation for concrete compared to abstract words in left ATL around 240 ms, and a reversed effect in right ATL around 340 ms. This biphasic pattern over time is similar to the results reported by Dhond et al. (2007), although our effects occurred earlier. This is consistent with the average behavioral responses in our study being faster by about 200 ms compared to the previous study. As the stimuli used in the present study were similar in length and lower in frequency than those used by Dhond et al. (2007), stimulus properties are unlikely to have caused this difference. Stimulus presentation durations may well have played a role, as these were 700 ms in Dhond et al. (2007) compared to only 150 ms here, which may have induced our participants to respond more quickly.

Dhond et al.'s (2007) interpretation of the initial concreteness effect in the left ATL and subsequent reversed effect in the right ATL was that initially concrete words are processed more effortfully by the left-lateralized verbal-linguistic system, and at a later

stage involve imaginistic processes in the right-hemisphere (Guo, et al., 2013; Paivio, 1991). We would like to suggest the alternative interpretation that concrete words engage the left ATL more early-on during processing due to their greater semantic richness (Harm & Seidenberg, 2004; Pexman, et al., 2008; Plaut & Shallice, 1993), while abstract words require more effort to recognize which then recruits additional resources for these items in the right ATL. Although fMRI studies have generally reported left hemisphere concreteness effects (Fiebach & Friederici, 2004; Sakreida, et al., 2013), such studies report effects that are a summation of processes occurring over a much longer time window than those considered here.

The hierarchical organization of the visual processing stream along a posterior-to-anterior gradient is well-established, at least for object processing (Riesenhuber & Poggio, 2002); but it is still unclear how, where and when visual information connects with networks representing semantic information, which is generally assumed to be distributed across multiple brain regions. Our data suggest that this connection is established primarily by the anterior temporal lobe around 240 ms after stimulus presentation. This latency is well before the peak of the N400 component which is traditionally associated with semantic word processing (Kutas & Federmeier, 2011; Lau, Phillips, & Poeppel, 2008). Several studies have suggested a contribution of ATL to the N400 component (Halgren, et al., 2002; Lau, et al., 2008; Nobre & McCarthy, 1995), and a recent MEG study reported masked semantic priming effects in ATL in the N400 latency range between 300-500 ms (Lau, Gramfort, Hamalainen, & Kuperberg, 2013). We do not believe that our effects around 240 ms simply reflect an “onset” of the N400, since we found a different pattern of results around 340 ms. We propose that activation at later latencies reflects processes beyond the single word level, such as combinatorial semantics or context integration, possibly also involving the ATL.

Semantics is not a unitary phenomenon, but consists of multiple aspects operating at different time scales. For example, Barsalou (2008) argued for a distinction between an early “linguistic” and a later “conceptual simulation” phase during semantic processing. This highlights the necessity to use time-resolved neuroimaging methods such as EEG/MEG, since particular brain regions may subserve different functions at different latencies. We propose that our effect at 240 ms corresponds to the early linguistic stage, and in computational terms reflects the operation of a hidden layer in a connectionist network through which word forms are integrated with more neurally distributed aspects of semantic representation. In this respect, we may have uncovered the hidden layer of semantics, and hope that this will promote new opportunities to link computational modelling with brain imaging.

Acknowledgments

This work was supported by the Medical Research Council UK (MC-A060-5PR40 to OH; PhD scholarships of the Cambridge Overseas Trust, Caius College Cambridge and MRC-UK to YC) and Experimental Psychology Society Study Visit Grant to GE.

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Figure legends:

Figure 1:

A) Time-course of word-evoked activation. The root-mean-square (RMS) of signal-to-noise ratios (SNR) was computed over time for LexD and SemD separately. Computation of SNRs allows the combination of different sensor types into one curve.

B) Minimum norm estimates of brain activity averaged across all stimuli in LexD at selected latencies after word presentation are displayed on the inflated average cortical surfaces for the left and right hemispheres, respectively. At 340 ms, three ROIs that were included in our main ANOVA model are indicated in white, while additional ROIs that were tested individually are indicated in grey. Time courses of mean activations within ROIs are shown in separate images. vOT: ventral occipito-temporal cortex; IT: inferior temporal cortex; AT: anterior temporal lobe; IF: inferior frontal gyrus; PC: Precentral; IP: Inferior parietal.

Figure 2: Time course of differential source activation in LexD.

Difference distributions for minimum norm estimates in the left cortical hemisphere for the main effects of Typicality (Typical minus Atypical) and Context (Pseudoword minus Pseudohomophone Context), and the interaction Context-by-Lexicality (Words minus Pseudowords in PW and PH context, respectively).

Figure 3: Time course of differential source activation in SemD.

Difference between minimum norm estimates between concrete and abstract words in the SemD task, for the left and right cortical hemispheres separately.

Figure 4: Statistical ROI analysis in source space.

A) Significant ANOVA results for three ROIs in left temporal lobe in different latency ranges for the Lexical Decision task.

B) Significant ANOVA results for brain activation in left and right ATL in the Semantic Decision task.

Panel labels indicate latency ranges and significant main effects or interactions. */o: significant or marginally significant, respectively. Units are in pA. ATL: Anterior temporal lobe; ITC: inferior temporal cortex; vOTC: vento-occipito-temporal cortex.

Tables

Table 1A. Means (and standard deviations) for a range of psycholinguistic variables for the lexical decision stimuli as a function of typicality, lexicality and task context.

	Nonword Set				Pseudohomophone Set			
	Nonwords		Words		Pseudohomophones		Words	
	Atypical	Typical	Atypical	Typical	Atypical	Typical	Typical	Atypical
Written Frequency	NA	NA	8.04 (8.25)	11.64 (9.96)	NA	NA	8.45 (9.70)	12.28 (16.82)
Letters Changed	1.17 (0.38)	1.21 (0.42)	NA	NA	1.13 (0.34)	1.21 (0.42)	NA	NA
Type Letter Frequency	364.4 (134.6)	674.1 (234.9)	388.4 (149.1)	696.7 (233.6)	444.9 (169.2)	709.8 (311.7)	381.1 (148.4)	627.8 (218.4)
Token Letter Frequency	4495.4 (1717.2)	8248.4 (2219.5)	4669.6 (1649.9)	8570.5 (2585.5)	5158.3 (1980.9)	8040.4 (2020.4)	4414.8 (1867.5)	7618 (2250.5)
Type Bigram Frequency	20.5 (10)	88.3 (25.8)	22.1 (9.8)	97.7 (25.4)	22.7 (9.6)	89.5 (58.7)	22.3 (10.4)	86.8 (33.4)
Token Bigram Frequency	197.7 (154.9)	1461 (826.6)	227.9 (159)	1605.6 (959.6)	233.7 (168.3)	1274.2 (524.9)	216.7 (124.4)	1384.2 (574.4)
Type Trigram Frequency	2.6 (2.4)	14.3 (6.4)	3.5 (2)	16.6 (7.2)	3 (2)	12 (7.2)	4 (2.4)	12.8 (6.4)

Token Trigram Frequency	14.8 (14.1)	213.7 (137.7)	22.7 (17)	237.5 (121.5)	18.6 (25)	212.2 (154.8)	26.3 (20.7)	220.9 (135.3)
Neighbourhood Size	1 (0.9)	2.3 (2.2)	0.5 (0.9)	2.2 (1.9)	1 (0.5)	3 (3.3)	0.5 (1)	2 (2.6)
Neighbourhood frequency	5.4 (10.7)	17.8 (30.8)	0.6 (1.3)	21 (32.7)	7.6 (9.9)	30 (44.3)	1.2 (3.5)	10.5 (18.1)

Table 2. Means (and standard deviations) for a range of psycholinguistic variables for the semantic decision stimuli as a function of concreteness.

	Concrete	Abstract
Number of Letters	5.9 (0.8)	6 (0.8)
Number of Phonemes	5 (1.2)	5.2 (1.2)
Number of Syllables	2 (0.6)	2.1 (0.8)
KF Frequency	15 (18)	15 (15)
CELEX Frequency	12 (15)	15 (14)
Familiarity Rating	462 (59)	447 (98)
Concreteness Rating	590 (26)	303 (39)
Imageability Rating	566 (41)	388 (78)

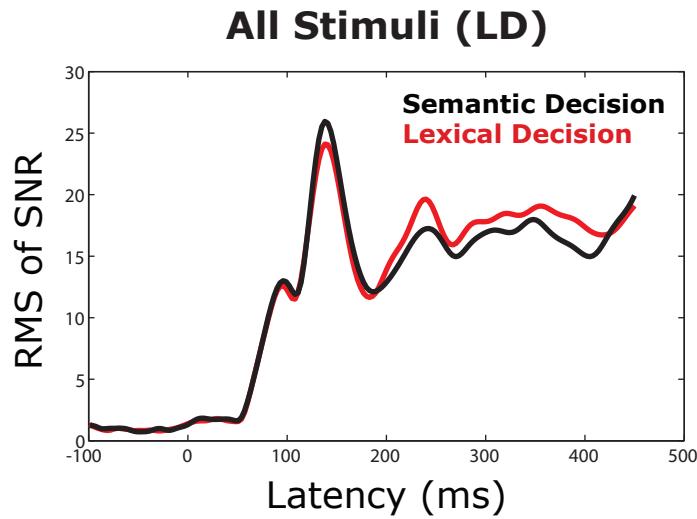
Note: KF (Kucera-Francis) Frequency, Familiarity, Concreteness and Imageability values taken from the MRC Psycholinguistic Database (Coltheart, 1980) and CELEX Frequency taken from the MCWord Database (Binder & Medler, 200X)

Table 3. Mean reaction times and error rates in the lexical decision task (with standard deviations) as a function of typicality, lexicality and context.

			Reaction Time (ms)	Error Rate (%)
Nonword Set	Nonwords	Atypical	752 (131)	5.39 (4.83)
		Typical	753 (154)	6.86 (7.36)
	Words	Atypical	691 (124)	7.35 (6.17)
		Typical	699 (132)	5.39 (5.66)
Pseudohomophone Set	Pseudo- homophones	Atypical	780 (97)	14.95 (9.21)
		Typical	822 (99)	18.87 (10.63)
	Words	Atypical	704 (88)	5.15 (5.99)
		Typical	740 (112)	11.52 (10.57)

Figure 1

A)



B)

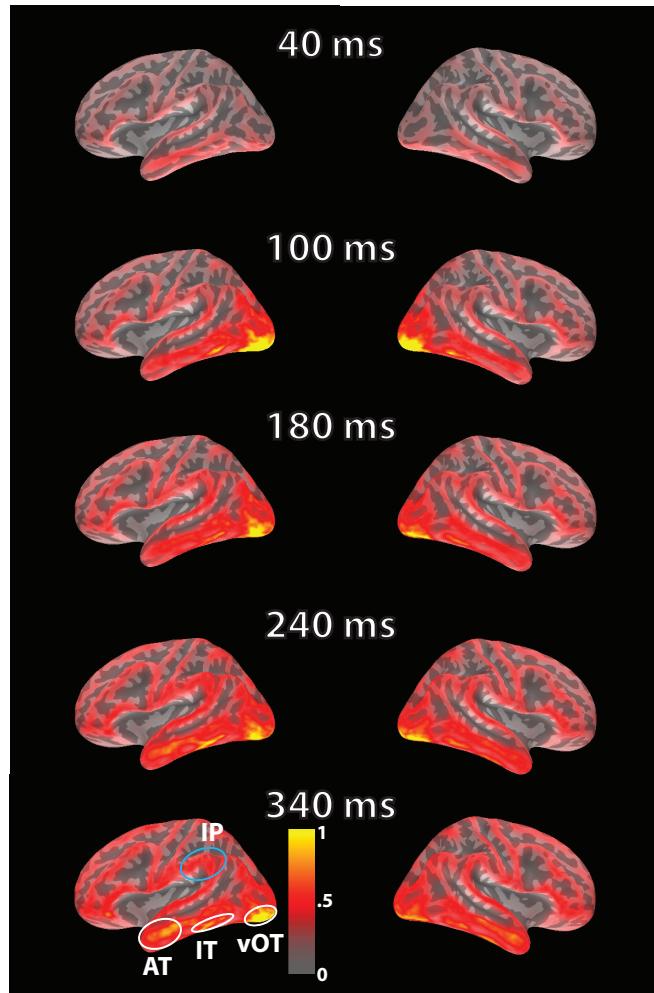


Figure 2

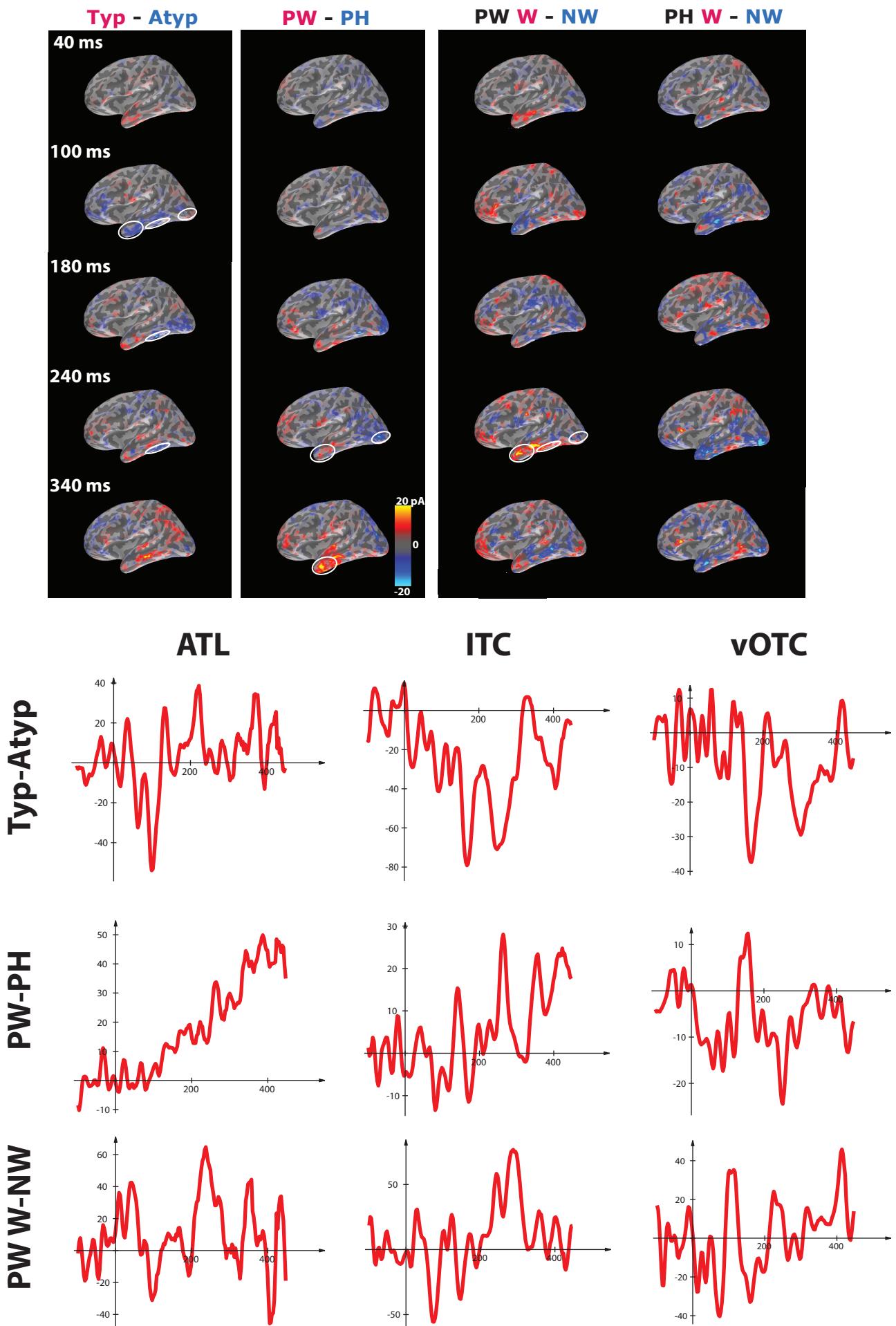


Figure 3

Lexical Decision

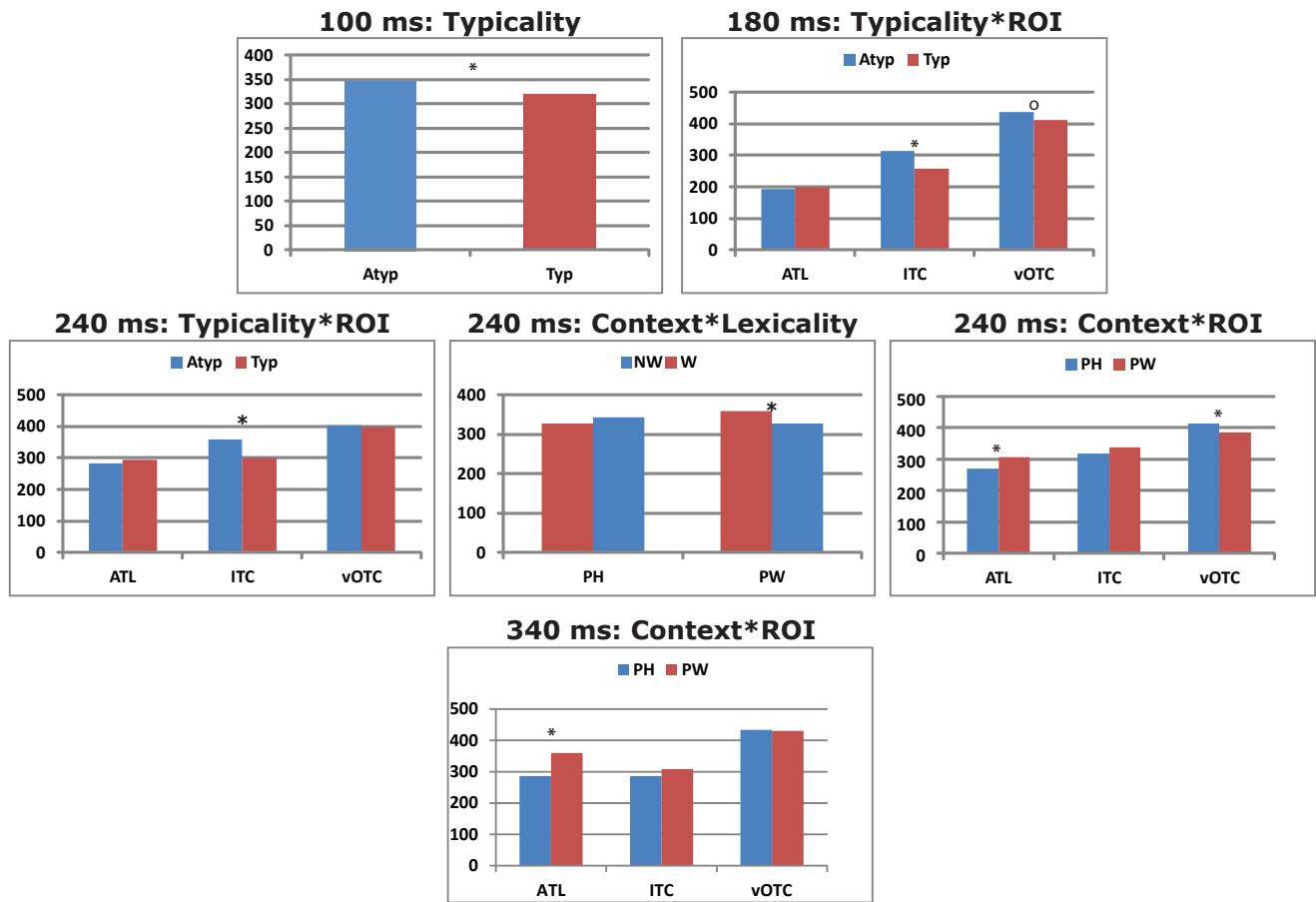
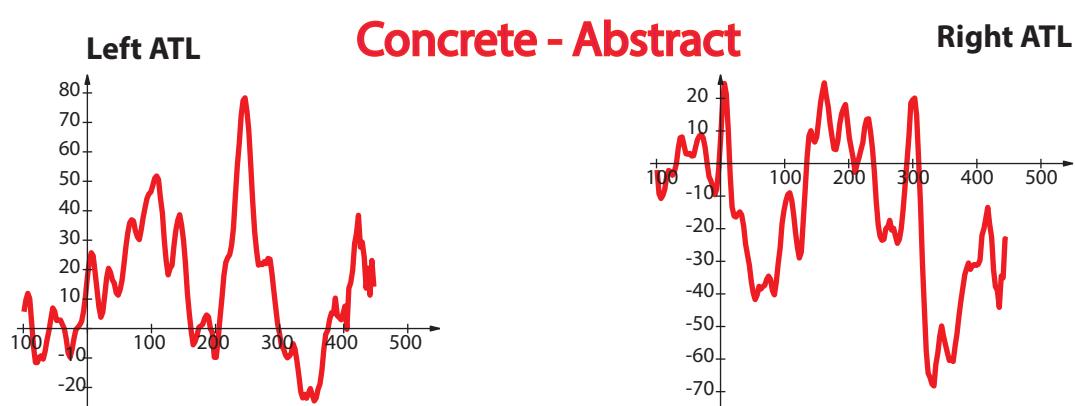
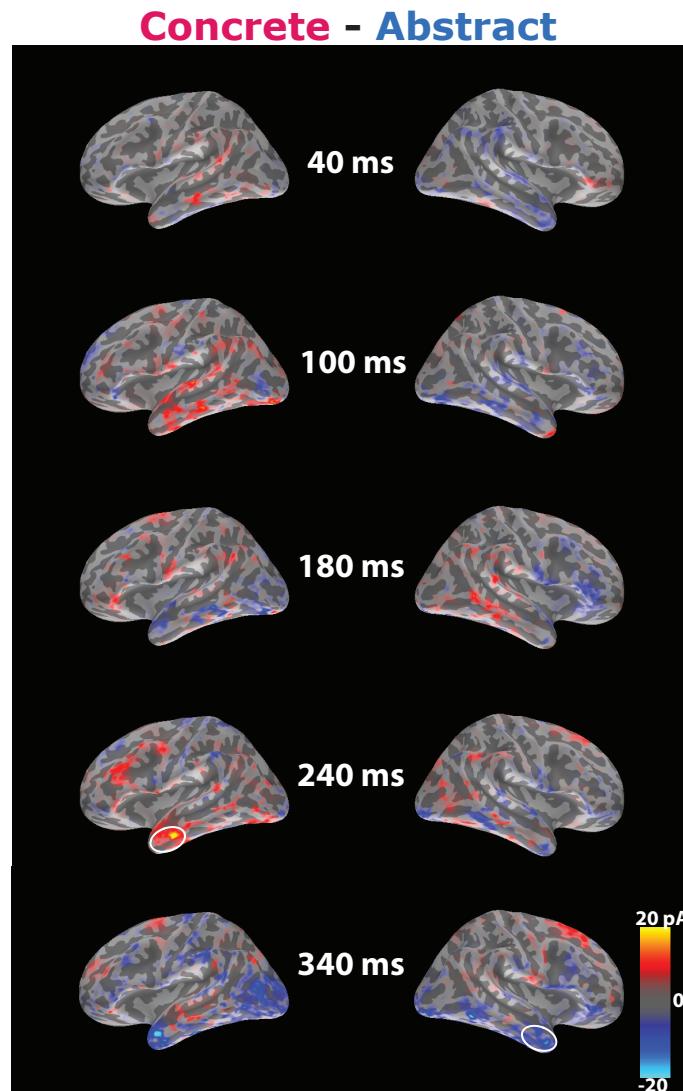


Figure 4

A) Lexical Decision



B) Semantic Decision

