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Title:

Early activity in Broca's area during reading reflects fast access to articulatory codes from print

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Abstract

Prior evidence for early activity in Broca's area during reading may reflect fast access to articulatory codes in left inferior frontal gyrus pars opercularis (LIFGpo). We put this hypothesis to test using a benchmark for articulatory involvement in reading known as the masked onset priming effect. In masked onset priming, briefly presented pronounceable strings of letters that share an initial phoneme with subsequently presented target words (e.g., *gilp-GAME*) facilitate word naming responses compared with unrelated primes (*dilp-GAME*). Crucially, these priming effects only occur when the task requires articulation (naming), and not when it requires lexical decisions. A standard explanation of masked onset priming is that it reflects fast computation of articulatory output codes from letter representations. We therefore predicted i) that activity in left IFG pars opercularis would be modulated by masked onset priming, ii) that priming-related modulation in LIFGpo would immediately follow activity in occipital cortex, and iii) that this modulation would be greater for naming than for lexical decision. These predictions were confirmed in a magnetoencephalography (MEG) priming study. Masked onset priming effects emerged in left IFG at around 100 ms post-target onset, and the priming effects were more sustained when the task involved articulation.

Key words: beamforming, MEG, masked onset priming, MOPE, inferior frontal gyrus pars opercularis, Broca’s area

Introduction

An increasing number of neurophysiological studies have reported very early activity (around 100ms after the onset of word presentation) in Broca's area (Broca, 1865) during reading (Pammer et al., 2004; Cornelissen et al., 2009, Wheat et al., 2010; Woodhead et al., 2012; Yvert et al., 2012). This early frontal activity is at odds with traditional views on the neural organization of reading that place access to a word’s phonetic representations rather later in time (around 400ms). Hence, the cognitive processes underlying this early activity are disputed. Recently, Broca's area has also been shown to be sensitive to phonological priming within the same early time period (Wheat et al., 2010), suggesting that this activity reflects fast access to phoneme representations from printed words. This would result from optimization of the mapping of orthographic representations onto articulatory codes for fluent reading aloud.

In the present study we use a benchmark phenomenon for the involvement of articulatory processes during reading, the masked onset priming effect (MOPE), in order to test the above account of early activity in Broca's area. Masked onset priming refers to the observation that words are read aloud faster when they are preceded by visually masked primes that share the same initial phoneme (e.g., *gilp-GAME*) compared with primes that begin with a different phoneme (e.g., *dilp-GAME*). The effect has been reported in several behavioral studies (e.g., Schiller, 2008; Schiller, 2007; Carreiras et al., 2005; Kinoshita, 2000, 2003; Grainger and Ferrand, 1996; Forster and Davis, 1991). Grainger and Ferrand (1996) proposed an account of masked onset priming according to which letter-level representations connect directly with phoneme-sized representations involved in planning an articulatory response (see Fig. 1). This proposal was adopted by Kinoshita and colleagues in subsequent work and referred to as the speech planning account of masked onset priming (Kinoshita, 2000; Kinoshita and Woolams, 2002; Malouf and Kinoshita, 2007).

Insert Figure 1 here

The key characteristic of the masked onset priming effect that supports a speech-planning account is that such priming effects are observed only in tasks that require an articulatory response and not in those that do not, such as lexical decision (Carreiras et al., 2005; Forster and Davis, 1991; Grainger and Ferrand, 1996; Schiller, 2008). Our study builds on this characteristic of masked onset priming, and uses magnetoencephalography (MEG) in order to test the hypothesis that early activity in Broca's area (more precisely, LIFG pars opercularis), seen upon presentation of a printed word, reflects the fast mapping of orthographic representations onto articulatory codes in preparation for reading aloud. If this is indeed the case, then we should see early modulation of activity in this specific region (LIFG pars opercularis) by masked onset priming. Furthermore, we expect this modulation of LIFGpo activity to be greatest when the task requires articulation, and we expect LIFGpo activity to arise soon after the earliest evidence for letter-level processing in middle occipital gyrus (Tarkiainen et al., 1999; Cornelissen et al., 2003).

Materials and Method

Initial Behavioral Experiment

Our MEG experiment is predicated on the idea that a masked onset priming effect occurs when the experimental task requires overt naming and therefore articulation of printed words, but not when the task is lexical decision which does not require articulation (Carreiras et al., 2005; Grainger and Ferrand, 1996). We conducted an initial behavioral-only experiment to both replicate this effect (in order to demonstrate that our experimental design and stimuli produce the MOPE as reported in the literature) and to allow identification of candidate participants for MEG.

Participants

Forty-eight native English-speaking, strongly right-handed adults (mean age: 20.9 years, SD: 3.23 years, 27 female) participated in the initial behavioral experiment. None had been diagnosed with reading disabilities and all read normally based on TOWRE and TIWRE performance (Torgesen et al. 1999, Reynolds and Kamphaus, 2007). Handedness was defined by the Annett Hand Preference Questionnaire (Annett, 1967).

Stimuli

Participants performed two tasks, word naming and lexical decision, in two different experimental sessions. Both sessions employed the same four conditions: a masked onset priming condition in which word targets shared their onset with the prime ("bude"-"BANK", ONSET-WORD); a control condition in which word targets had a different onset from the prime ("wude"-"BANK", CONTR-WORD); two analogous conditions using nonword targets ("boik"-"BAME", ONSET-NONW; "loik"-"BAME", CONTR-NONW). The nonword targets were necessary for the lexical decision task and were therefore included in the naming experiment to keep the pattern of stimulus presentations identical across tasks (but they were not analyzed). The target stimuli were 112 English four-letter real words and 112 English four-letter nonwords selected from the English Lexicon Project (Balota et al., 2007). 224 English nonwords served as primes. Half of these nonwords (112) were selected from the English Lexicon Project and then re-used to create the remaining 112 nonword primes by changing their onset (e.g., "bude" was used as the basis for "wude"). Word targets were restricted to singular nouns, noninflected verbs, and adjectives. The KF frequency (Kučera and Francis, 1967) of all real words was above 30 per million (mean word frequency count of 155.83). The mean reaction times in word naming (according to the English Lexicon Project) was between 516.0ms and 666.95ms with a mean of 574.35ms. No words were selected that had a mean lexical decision accuracy below 95%. All stimuli (words and nonwords, primes and targets) were monosyllabic with simple onsets comprising one consonant followed by one vowel. To avoid missing reaction times due to voice-key failures and to prevent ambiguous pronunciation of nonwords, we did not use any stimuli starting with the letters: “c”, “f”, “h“, “q”, “s”, “x”, “y”, and “z”.

In order to make the design as balanced as possible, all targets and all primes were presented in all conditions to each individual participant. This was accomplished by creating groups of four target items with the greatest possible overlap in letter and letter position (apart from the onset) and a corresponding group of four prime items which had no other letter in common with any word of the items in its target group (apart from the onset). Each of the two groups had two items with one onset and two items with another, matching the onset in the other group, e.g., LAKE, LANE, GAME, GATE (targets) and lilp, lops, gilp, gops (corresponding primes). Hence each item of the prime group could be paired with each item of the target group in one of the four conditions (NAM-shared onset, LEX-shared onset, NAM-non-shared onset, LEX- non-shared onset). The lack of any overlap between the letters of the prime and the target items, beyond the first letter, was necessary to ensure that the priming effect could be attributed to the onset alone. Ten native speakers of English judged whether any of the nonwords sounded like real words and whether the pronunciation of nonwords was consistent (in particular whether prime and target onsets had the same pronunciation in the shared onset condition and a different one in the different onset condition).

Procedure

A pair of nonius lines was present on screen throughout each session in order that participants could fixate. On each trial, in the space between the nonius lines, and centered on the middle of the screen, the following sequence of events was presented: 500 ms forward mask “#####”, 60 ms lower case prime, 20 ms backward mask “#####”, 500 ms upper case target word. Subsequently, nothing was presented except for the nonius lines for 1500 ms. Stimuli were presented in Arial Monospace (24 pt) in light grey on a dark background using Presentation v12.0 (Neurobehavioural Systems) at a viewing distance of ~60 cm on a CRT monitor. The screen resolution was 1024 x 768 True Colour (64-BIT) with 100 Hz vertical refresh, allowing events to be manipulated in multiples of 10 ms increments. The timing of all events was locked to the vertical screen refresh. Participants were asked to read the words aloud as fast and as accurately as possible during the naming condition and to press the right button for words and the left button for nonwords as fast and as accurately as possible during lexical decision. Button box responses were recorded using a bespoke button box linked to the computer via the parallel port, which performed debouncing in hardware. Each session consisted of 448 trials.

Before the task began, the task was explained to the participants who were made aware that they might notice some flickering immediately prior to the target words. After the experiment was completed, prime visibility was informally assessed by interviews with the participants almost all of whom reported that they could not consciously perceive more than a flicker.

Data Analysis and Results

For the lexical decision task, the data showed similar mean response times for the shared onset condition (mean 477.4 ms, SD 80.4 ms) and the control condition (474.1 ms , SD 81.7 ms). For the naming task, however, a clear decrease in reaction times could be observed in the shared onset condition (mean 469.9 ms, SD 67.9 ms) in comparison with the control condition (mean 482.5 ms, SD 65.0 ms). A two-by-two repeated measures ANOVA with the within-participant factors of Task and Prime Type was computed. There was no statistically significant main effect of Task, F(1,47) = 0.002, p = 0.962, ηp2 = .000. However, there was a statistically significant main effect of Prime Type, F(1,47) = 13.53, p = 0.001, ηp^2 = 0.22, and a significant interaction between Prime Type and Task, *F*(1,47) = 48.41, p < 0.001, ηp^2 = 0.51. We computed all pairwise comparisons, using the Tukey-Kramer adjustment for multiple comparisons. Only the difference between shared onset and different onset conditions for naming was statistically significant at p < .001. No other pairwise comparison was statistically significant. These results demonstrate, for our stimuli and experimental design, a clear difference between the shared onset and different onset masked priming conditions of 12.6 ms for naming (effect size r = 0.72), but not for lexical decision.

MEG study

Participants

Since this study involved overt articulation in MEG, we expected a high attrition rate of participants due to movement artifacts. The threshold for tolerable movement over the course of a single MEG recording session was set at 1cm or less (for any individual electrode in 3d-space). This limit is a trade-off between the size of the beamformer reconstruction grid (5mm) and the expected degree of movement whilst performing overt articulation, and is consistent with previous published MEG work (e.g., Wheat et al., 2010). Based on theoretical considerations and previous experiments (e.g., Cornelissen et al., 2009, Wheat et al., 2010), we decided a priori to acquire complete and viable data sets for twenty participants. To select participants for scanning from the original sample of 48 who were tested behaviorally, we required that: a) individuals were suitable for MRI/MEG scanning, had given consent to be scanned and were available on specific dates (5 participants were excluded on this basis) and b) from the analysis of the individual behavioral data, that the mean difference between the participant's shared and different onset reaction times (for word or nonword naming) should be greater than or equal to the median group difference (10.6 ms) i.e., that individually there was evidence of a priming effect. In order to be able to use the MOPE as a benchmark phenomenon (to investigate the nature of the early Broca activation), it was important that participants produced a reliable MOPE behaviorally outside the scanner because it was not possible to combine reaction time measurement and MEG recording, without contaminating the signals with movement artifacts. According to these criteria, we identified 32 participants who were suitable for scanning. We then scanned these in random order until we had the requisite sample of 20 participants whose head movements were within the acceptable range (as described above). Of those participants who were able to consciously perceive the primes in the behavioral study none remained in the final sample, since they did not pass these criteria. The final twenty participants whose MEG data were analyzed were all native English speaking, strongly right-handed adults (mean age: 21.8 years, SD: 4.48 years; 11 female). All participants gave informed consent and the study conformed to The Code of Ethics of the World Medical Association (Declaration of Helsinki). For the 12 participants rejected because of excessive head movement and the final sample of 20, we compared the differences between shared and different onset reaction times (i.e. the priming effect) for naming (means: 16.3 versus 20.5; t(30)=1.02, p=0.31) and lexical decision (means: 4.9 versus 4.8; t(30)=0.01, p=0.99). The absence of a statistically significant difference in each case suggests that there was no systematic sampling bias in terms of behavioral performance for the participants who contributed to the final MEG dataset.

Stimuli

This MEG study comprised two separate scanning sessions: a naming session and a lexical decision session the order of which was counterbalanced across participants. The stimuli for these were identical to the two sessions in the behavioral experiment, except for a new random order.

Procedure

To minimize movement artifacts caused by overt spoken responses, participants used a bite bar. In addition, overt responses to the stimuli were delayed. For word naming, participants were asked to read target words aloud only when they were prompted with a question mark "?", which occurred 1300 ms after target onset. Similarly, in the delayed lexical decision experiment, participants were asked to press the right button for words and the left button for nonwords, but only when the question mark prompt appeared. Delaying overt responses in this way allows for a clear separation of the neural correlates of stimulus encoding and response planning from response execution (cf. Salmelin et al., 2000). During the naming experiments in the MEG scanner, participants could be heard over an intercom at all times, ensuring they were reading words aloud, that their pronunciation was approximately correct (deviations were expected due to the bite bar), and that they responded within the desired time window (in particular that they did not respond before the response prompt). As in the behavioral experiment, each scanning session (i.e., each task) consisted of 448 trials. A pair of nonius lines was present on screen throughout each session in order that participants could fixate. On each trial, in the gap between the nonius lines, and centered on the middle of the screen, the following sequence occurred: 500 ms forward mask “#####”, 67 ms lower case prime, 17 ms backward mask “#####”, 500 ms upper case target word, 800 ms delay, 1200 ms question mark “?”, and 800 ms blank (except for the nonius lines) to which a random jitter time of 100-1000ms was added. Stimuli were back-projected (60 Hz vertical refresh) as light grey words and symbols (Arial Monospace, 24 pt) on a dark gray background using Presentation v12.0 (Neurobehavioural Systems). At a viewing distance of ~75 cm stimuli subtended ~1° vertically and ~5° horizontally.

Data acquisition

MEG data were collected continuously using a 4D Neuroimaging Magnes 3600 Whole Head, 248 channel system, with the magnetometers arranged in a helmet shaped array. Data were recorded with a sample rate of 678.17 Hz and were filtered online with a 200 Hz lowpass filter. Three bad channels were identified and excluded from all levels of the data analysis for all participants. Head shape and head coil position were recorded with a 3-D digitizer (Polhemus Fastrak).

Artifact Rejection

Every channel for every trial was inspected and epochs containing artifacts, such as blinks, articulatory movements, swallows, and other movements, were rejected manually. For the naming task 11.1% (SD 6.1%) of trials on average were rejected as compared to 10.8% (SD 8.4%) for lexical decision. There was no statistically significant difference in these rejection rates (t(19)=0.16, p=0.87). Head movement was assessed by measuring the location of 5 fiducial coils at the start and end of each run. As stated, movement > 1cm resulted in rejection. However, no online head movement tracking was used.

Beamforming method

For the source-space analyses, head-shape and head-coil positions were coregistered with the individual participants' anatomical magnetic resonance (MR) scans using a surface-matching technique adapted from Kozinska et al. (2001). High-resolution T1-weighted MR images (reconstructed to 1 mm isotropic resolution) were acquired with a GE 3.0-T Signa Excite HDx system (General Electric, Milwaukee, USA) using an 8-channel head coil and a 3-D fast spoiled gradient recall echo sequence. The parameters were TR/TE/flip angle = 7.8 ms/3 ms/20°, spatial resolution of 1.13 mm× 1.13 mm× 1.0 mm, in-plane resolution of 256 × 256 × 176 contiguous slices, FOV of 290 x 290 x 176.

Neural sources of activity were reconstructed with an in-house modified type I vectorized linearly constrained minimum-variance beamformer (Van Veen et al., 1997; Huang et al., 2004) with a multiple spheres head model (Huang et al., 1999). In a beamforming analysis, the neuronal signal at a point of interest in the brain is constructed as the weighted sum of the signals recorded by the MEG sensors, the sensor weights computed for each point forming three spatial filters, one for each orthogonal current direction. The beamformer weights are determined by an optimization algorithm so that the signal from a point of interest contributes maximally to the beamformer output, whereas the signal from other locations is suppressed. For a whole-brain analysis, a cubic lattice of point sources is defined within the brain (with 5 mm spacing) and for each point source, a set of spatial filters is defined which estimates the source current at each grid point. An independent set of weights is computed for each point. The outputs of the three spatial filters at each point in the brain are then summed to generate the total power (i.e. combining both phase-locked and non-phase-locked signal components) at each so-called "virtual electrode" (VE) over a given temporal window and within a given frequency band (see Huang et al., 2004 p142, eqns. 11 and 12).

For the group analyses in MEG source-space, each individual's MEG data were co-registered with their MRIs and then spatially normalized to the Montreal Neurological Institute (MNI) standard brain, based on the average of 152 individual T-1 weighted structural MR images (Evans et al., 1993). The beamformer grid for each participant was initially defined in MNI space and transformed back to each individual's MRI. The beamforming was then performed in the individual's MRI space on these transformed grids, and then the subsequent t-maps were transformed into MNI space before group-statistics are calculated.

Beamforming statistics

For the initial, within participant level of statistical analysis, a paired-sample t-statistic between active and passive conditions for each point in the 5mm beamformer grid was computed in particular frequency band/time windows (see below for justification of specific frequency band and time window combinations). For each participant, for each contrast, at each of the frequency band/time window combinations, this procedure generated separate t-maps. We then used a multistep procedure (Holmes et al., 1996) at the group level of statistical analysis in order to compute a permutation distribution of the maximal statistic from the population of VEs in MNI space (Nichols and Holmes, 2004). This was calculated by relabeling the experimental conditions, so that for a single VE, under the null hypothesis, the t-distribution would have been the same irrespective of label. In our case the maximal statistic was the largest mean t-value averaged across participants. For the group analysis, if the maximal statistics for the actual labeling of the experiment was in the top 5% of the permutation distribution, we rejected the omnibus hypothesis, i.e. that all the VE null hypotheses are false. This procedure has been previously shown to have robust control over experiment-wise type I error (Holmes et al., 1996).

Time–frequency analysis: whole brain

After pre-processing, the MEG data were segmented into epochs running from 850 ms before target onset to 850 ms after. Previous MEG studies of visual word recognition have revealed a complex spread of activity across the cortex with time (Tarkiainen et al., 1999; Pammer et al., 2004; Cornelissen et al., 2009). The earliest components of this pattern occur in occipital, occipitotemporal, and prefrontal cortex ~100–150 ms after stimulus. Therefore, as a compromise between being able to reveal this temporal pattern across the whole brain and being able to resolve oscillatory activity as low as 5–15 Hz, we conducted beamforming analyses for 200-ms-long windows. At the first, within-participant level of statistical analysis, we computed a paired sample t-statistic for each point in the virtual electrode grid. To do this, we compared the mean difference in oscillatory power (averaged across epochs) in four frequency bands (using fourth order Butterworth filters with automatic padding): 5–15 Hz, 15–25 Hz, 25–35 Hz, and 35–50 Hz between a 200 ms passive window (i.e., 800 to 600 ms before target onset), which was shared between all conditions, and five active time windows (0–200, 100-300, 200-400, 300-500, and 400-600 ms following target onset). These beamforming parameters were chosen to be the same as those used in several recent MEG studies of visual word recognition (e.g. Pammer et al., 2004; Cornelissen et al., 2009; Wheat et al., 2010) in order to allow a comparison of our results with these studies. Moreover, the point of interest analyses in Fig. 4 show that the significant differences between experimental conditions which we found during the first 500 ms following target onset occurred between 5-50 Hz. Therefore, the choice of frequency bands for the whole brain analysis has not missed important information in the data.

Time frequency analysis: points of interest (POIs)

We wanted to compare the total oscillatory power between experimental conditions, retaining millisecond temporal resolution, at two points of interest (POI): 1) the LIFGpo which is the main site of interest for the current study, and 2) a comparison area, left middle occipital gyrus (LMOG) which is the first component of the visual cortex which has been shown to be sensitive to orthographic processing (Tarkiainen et al., 1999; Cornelissen, 2010). Time-frequency analyses were computed using mean coordinates for LIFGpo [-55.8, 4.6, 20.8] and LMOG, [-22.6, -95.4, 3.4] based on regions of interest that have been reported in three other beamformer-based MEG studies of visual word recognition (Pammer et al., 2004; Cornelissen et al., 2009; Wheat et al., 2010).

Once selected, the MNI co-ordinates for the two POIs were transformed back into individual space so that virtual electrodes could be applied at these point sources in each individual's brain to reconstruct the time series at each POI. The beamformer methods were the same as those used for the whole brain analysis. However, for the POIs, they were applied over the time window from 850ms before target onset to 850ms following. We then used Stockwell transforms (Stockwell, 1996) to compute time-frequency plots for the total power over a shorter time window from -50 to 800 ms, (to avoid edge artefacts) for the whole range of frequencies from 5-50 Hz. The time frequency plots were normalized, separately for each condition and for each participant, by the mean power per frequency bin over the same baseline as was used for the whole brain analysis (i.e. 800ms to 600 ms before target onset). The percentage signal change between conditions was then computed from the normalized data. The separate plots were then compared statistically to identify regions in the time-frequency space where the total power at the two POIs was significantly modulated by priming and task.

These statistical comparisons were made using PROC MIXED in SAS (SAS Institute Inc., North Carolina, US) to compute a generalized linear mixed model (GLMM). In the GLMM comparing the different stimulus conditions a repeated measures factor was included to account for the fact that each participant’s time-frequency plot is made up of multiple time-frequency 2D arrays. We controlled for time-frequency co-variance in the spectrograms by assuming the estimates of power followed a Gaussian distribution. A Gaussian link function was therefore used in the model for the outcome. To correct for the spatial auto-correlation within the spectrogram an exponential spatial correlation model for the model residuals was integrated into the overall model (Littell et al., 2006). Lsmean estimates of percentage signal change that were either statistically significantly greater or less than 1 (α=0.05), after correcting for multiple comparisons, are reported.

Results

Behavioral Data

The twenty participants of the initial behavioral experiment who showed robust MOPE effects and who did not have excessive head movement during MEG scanning were analyzed in detail. Note that these behavioral data are from participants that have been selected to produce a MOPE. We report them to describe the effect size that these particular participants produce and not to demonstrate a MOPE in general, since this effect is sufficiently established in the literature. Below we present their reaction time (RT) data from the initial behavioral study. Inside the MEG scanner participants were instructed to give a delayed response, so reaction times could not be analyzed.

Figure 2 about here

Once incorrect responses were removed, including failure to respond, the data were further filtered to exclude reaction times outside 3 SDs from the mean for each participant for each task and for each condition. The mean attrition rates for lexical decision and naming tasks were 1.5% (0.5% - 2.3%) and 1.6% (0.5% - 3.2%) respectively.

For the lexical decision task, the data showed similar mean response times for the shared onset condition (mean 472.3 ms, SD 100.0 ms) and the control condition (mean 467.5 ms, SD 94.9 ms). For the naming task, however, a clear decrease in reaction times could be observed in the shared onset condition (mean 455.1 ms, SD 74.3 ms) in comparison with the control condition (mean 474.8 ms , SD 72.2 ms).

Figure 2 shows the mean reaction times for both priming conditions and both tasks. A two-by-two repeated measures ANOVA with the within-participant factors of Task and Prime Type was conducted. The results showed no significant main effect of Task, $F(1,19) = 0.14$, $p = 0.709$, $\eta p^2 = 0.007$. However, there was a significant main effect Prime Type, $F(1,19) = 22.09$, $p < 0.001$, $\eta p^2 = 0.54$, and a significant interaction, $F(1,19) = 54.74$, $p < 0.001$, $\eta p^2 = 0.74$. We computed all pairwise comparisons, using the Tukey-Kramer adjustment for multiple comparisons. Only the difference between shared onset and control conditions for naming was statistically significant at $p < .001$. No other pairwise comparison was statistically significant.

Percent correct responses

For speeded responses outside of the scanner, the mean correct response rates for the control and shared onset conditions were 99.1% (range 88.4% – 100.0%) and 98.8% (range 84.8% - 100.0%) respectively in the naming task. In the lexical decision task the mean correct response rates for the control and shared onset conditions were 95.0% (range 81.3% – 100.0%) and 92.6% (range 79.5% - 98.2%) respectively.

For unspeeded responses in the scanner, the mean correct response rates in the naming task for the control and shared onset conditions were 99.5% (range 97.3% – 100.0%) and 99.3% (range 96.4% - 100.0%) respectively, and the mean correct response rates in the lexical decision task were 96.16% (range 91.07% - 100.00%) and 96.94% (range 91.96% - 100.00%) for the control and shared onset conditions respectively. Naming errors were responses that were clearly wrong, responses that occurred before the question mark, responses that occurred too late after the question mark, and trials without any audible response. Lexical decision errors were wrong button presses, responses that occurred too early or too late, as well as trials without any button press.

Whole-brain MEG Data

Figure 3 shows the statistically significant changes in oscillatory power (thresholded at $p < 0.05$, whole-brain corrected) at the cortical surface comparing the four experimental conditions to a passive baseline.

Naming

As can be seen in Figure 3A, during the first 200 ms following target onset, in the naming task during the shared onset priming condition only occipital areas were activated. By the second time window, (100 - 300 ms) a response of the left inferior frontal gyrus (pars opercularis) emerges at 15 – 25 Hz. Thereafter, activity in this area becomes more extensive and can also be observed at 25 – 35 Hz. Similar results can be seen in Figure 3B for the control condition, although the prefrontal response is somewhat more posterior.

Figure 3 about here

Lexical Decision

When participants performed lexical decision, the shared onset and control conditions (compared to a passive baseline, thresholded at $p < 0.05$) showed a very different pattern, as can be seen in Figure 3C and D. While during the first time window (0 – 200 ms) the activity found in all frequency bands looks almost identical to the activity found during the naming task, as early as in the second time window (100 – 300 ms) it can be observed that in contrast to the naming task, there are no responses in prefrontal areas, the superior and inferior temporal gyri, nor the anterior temporal pole. Intriguingly, for the shared onset condition however, there is a later response at 200-400 ms with peak activity at the frontal pole in the 35-50 Hz frequency band.

Virtual Electrode Analysis of Points of Interest

We compared the responses in the time-frequency domain between experimental conditions at two regions of interest: the left middle occipital gyrus (LMOG, MNI: -22.6, -95.4, 3.4) and the left inferior frontal gyrus (LIFGpo, MNI: -55.8, 4.6, 20.8). The time-frequency plots for each of the four experimental conditions at each POI are available in the supplementary material.

Figure 4 about here

Fig. 4A shows group level time-frequency analyses of the percentage signal change between the shared onset and control conditions collapsed (i.e. averaged) across task, separately for LIFGpo and LMOG. Blue colors indicate a stronger decrease in power for the shared onset than the control conditions. The black contours show the regions in time-frequency space where this difference is statistically significant at $p < 0.05$. While Fig. 4A confirms the absence of a priming effect in LMOG, it does show a statistically significant main effect of priming in LIFGpo, with the shared onset priming condition generating a stronger response than the control condition in the 15-30 Hz frequency range in two periods from about 0 to about 150 ms and from about 400 to about 600 ms.

Fig. 4B shows the effect of priming in LIFGpo separately for the naming task (on the left) and the lexical decision task (on the right). From Fig. 4B it appears that there is a very early, statistically significant difference between shared onset and control priming for both naming and lexical decision, at around 50-130 ms in the 15-20 Hz frequency range. Thereafter, the statistically significant differences between shared onset and control conditions persist only for the naming condition, in the 15-35 Hz frequency range, right up to 500 ms after target onset. No equivalent differences between the priming conditions exist for lexical decision over the same time period.

Fig. 4C is a plot, in time-frequency space, of the difference in the strength of priming comparing naming with lexical decision. Specifically, it shows: (percentage signal change between shared onset and control for naming) minus (percentage signal change between shared onset and control for lexical decision). By inspection, this is equivalent to visually subtracting the right hand plot in Fig. 4B from the left hand plot in Fig. 4B. Statistically, Fig. 4C confirms what Fig. 4B already suggests: in the LIFGpo, the priming effect (i.e. shared onset versus control) differs significantly between naming and lexical decision only after around 200 ms, where the priming effect persists for naming, but not for lexical decision.

Discussion

The aim of the present study was to test the hypothesis that prior observations of early activity in Broca's area during reading (Pammer et al., 2004; Cornelissen et al., 2009; Woodhead et al., 2012;

Wheat et al., 2010; Yvert et al., 2012) might reflect the rapid computation of articulatory codes from print. To do so we used a benchmark for articulatory involvement in reading, the masked onset priming effect (MOPE). Masked onset priming refers to the behavioral facilitation in reading words that arises when target words are preceded by briefly presented pronounceable letter strings that share their initial phoneme with targets (onset primes) compared with completely unrelated primes. Crucially, this behavioral facilitation only occurs when the task requires articulation (naming), and is not observed during lexical decision tasks (Carreiras et al., 2005; Forster and Davis, 1991; Grainger and Ferrand, 1996; Schiller, 2008). This result supports a speech-planning account of masked onset priming (Grainger and Ferrand, 1996; Kinoshita, 2000), according to which masked onset priming reflects fast access to articulatory output representations from letter strings (see Fig. 1). We predicted that if the early activity in Broca's area (LIFGpo) during reading seen in prior research reflects the rapid access to articulatory codes from print, then we should be able to modulate this early activity by masked onset priming, and more so when the task involves articulation. Furthermore, the priming-related modulation of left IFGpo activity should rapidly follow activity seen in occipital cortex.

To test these predictions, we measured the MEG response to word targets that either had to be read aloud (naming) or classified as real words versus nonsense strings of letters (lexical decision). Word targets were preceded by briefly presented pronounceable strings of letters (primes) that could either share or not share the first phoneme with the following target word. Speeded behavioral responses recorded outside of the scanner revealed the classic masked onset priming effect, with faster naming responses following primes that share the first phoneme with target words, and no significant differences in lexical decision responses.

We analyzed whole-brain MEG activity as well as activity in two POIs of prior interest, LIFGpo and LMOG, using virtual electrode analyses. The results of the whole-brain analyses revealed a similar pattern of activity in occipital regions in the first time-window (0-200 ms) when comparing the shared onset prime condition with a passive baseline condition. Most important, with respect to the hypotheses under test, is that we only found evidence for priming effects in the LIFGpo virtual electrode analysis, and no such effects in the LMOG. In both tasks there was an early priming-driven modulation of activity in LIFGpo starting at around 100ms. Following that, however, only the naming task showed significant priming effects. The early onset of the modulation of spectral power in LIFGpo seen in both tasks supports the hypothesized direct link between letter-level representations and representations involved in the preparation of an articulatory response, and suggests that these feed-forward connections operate independently of the intention to articulate or not. Intention to articulate would, however, determine whether or not activity in articulation-related areas is sustained, and it is this sustained activity that would be the basis of masked onset priming effects seen in behavioral responses. A limitation of our results is that we did not extend our MEG measurements to participants who do not show a MOPE behaviorally. Had we recorded MEG responses in such individuals, we may have found: no effects; effects just like those that have been reported even in the absence of a behavioral response; or a very different pattern in MEG. Further study is required to address this question.

There is much evidence in support of the key role played by Broca's area (Broca, 1865) in the production of speech. Reviews of brain imaging research by Indefrey and Levelt (2004) and Hickok and Poeppel (2004, 2007) pointed to the posterior part of Broca's area (pars opercularis) as playing a central role in speech planning. This region is thought to be involved in the computation of articulatory codes by connecting phonological representations with their corresponding motor programs for articulation. In particular, the fMRI study of Papoutsi et al. (2009) provided strong evidence for the role of left IFG pars opercularis in the generation of an articulatory code.

The model shown in Figure 1 promotes direct fast links between sublexical orthography (letter-level representations) and articulatory preparation, which are supported by the fast frontal modulations we find in this study. Whether or not there is an anatomical pathway that implements such a direct connection between ventral occipito-temporal areas and IFGpo is a question that cannot be answered on the basis of our findings. Yet, the early onset of the modulation suggests a fast and rather direct anatomical connection. A plausible candidate for such a pathway is the left inferior fronto-occipital fasciculus (IFOF), a fiber bundle connecting occipital and ventral occipito-temporal areas with Broca's area (Curran, 1909; Anwander et al., 2007; Catani and de Schotten, 2008; Axer et al., 2012; Vandermosten, 2012). We note, however, that our data cannot exclude an alternative possibility: the early modulation of LIFGpo that we see at a whole brain level may in fact reflect the outcome of prior, ultra-rapid and much wider spread of activation throughout the reading network, but which is below the threshold for detection by whole-brain beamforming.

In our study participants processed stimuli with two different task instructions (naming vs. lexical decision). Hence, with the stimulation being identical, the sustained decrease of oscillations in the beta-band that we found in the naming task and not in the lexical decision task may be the result of task-driven, top-down processes geared to prepare LIFGpo for transforming bottom-up information into an articulatory response. This view is supported by Engel and Fries (2010), who reviewed a multitude of studies finding changes in beta-band activity and concluded that beta-band activation reflects the maintenance of the current sensorimotor or cognitive state by endogenous, top-down factors. Such endogenous influences would determine the relative impact of exogenous, bottom-up factors, with decreases in beta oscillatory activity signaling a greater role for the latter. Thus, in our study, the intention to articulate would have enabled a greater influence of bottom-up factors (i.e., priming) thought to affect activity in neural structures involved in generating an articulatory response. In line with this interpretation, a recent study of Gehrig et al. (2012) found that preparation for overt speech production was specifically associated with beta suppression in motor-related brain regions. This modulation of processing by task demands is also in line with other recent demonstrations of task effects on language-related processing (e.g., Strijkers et al., 2011). Our future work will focus on these intriguing influences of task demands on the modulation of early stimulus-driven neural activity.

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Figure Legends

Figure 1 A bimodal model of visual and auditory word recognition and naming adapted from Grainger and Ferrand (1996). Putative cortical areas are added based on literature reviews of reading, visual word recognition and speech processing (e.g., Guenther and Vladulish, 2012, Davis and Gaskell, 2009, Grainger and Ziegler, 2011). The figure illustrates our proposed account of masked onset priming according to which letter-level representations in occipital and ventral occipito-temporal areas connect directly with phoneme-sized representation in the inferior frontal gyrus.

Figure 2 Mean reaction times for the onset and control prime-target relations separately for lexical decision (LD) in gray bars and naming (NM) in white bars. The error bars represent the standard error of each mean corrected for repeated measures following Loftus and Masson (1994).

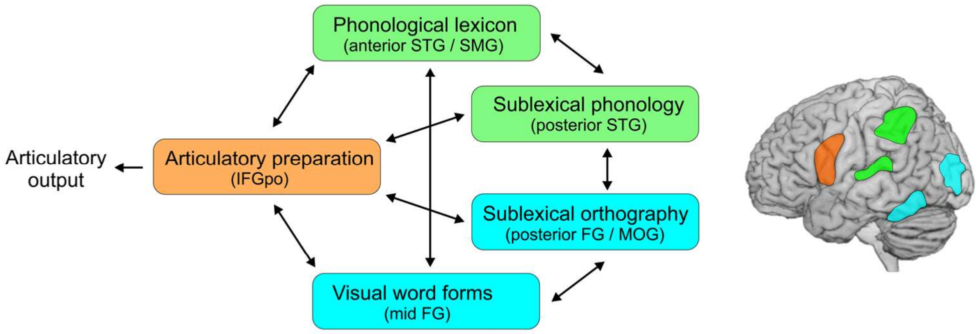
Figure 3 Three-dimensional rendered cortical representations showing oscillatory activity which is significantly different from baseline, thresholded at $p < 0.05$ (corrected). All the illustrated activations represent event related desynchronization (ERD). Time zero marks the onset of the target. A Naming, Shared Onset condition, four frequency bands and five (overlapping) early time windows. B Naming, Non-shared Onset condition, four frequency bands and five (overlapping) early time windows. C Lexical Decision, Shared Onset condition, four frequency bands and five (overlapping) early time windows. D Lexical Decision, Non-shared Onset condition, four frequency bands and five (overlapping) early time windows.

Figure 4 Time-frequency plots of percentage signal change for the left inferior frontal gyrus pars opercularis (LIFGpo) and the left middle occipital gyrus (LMOG). Black contours demarcate areas within which there is statistically significant percentage signal change between conditions/tasks ($p < 0.05$). A Main effect of Priming at LIFGpo and LMOG. These plots represent the difference between shared onset, averaged across task and nonshared onset, averaged across task. B Priming effects computed separately for each task LIFGpo. These plots represent the difference between shared onset and nonshared onset, separated by task (Naming and Lexical Decision). C Interaction between priming and task at LIFGpo. This plot represents the difference between the priming effect for naming and the priming effect for lexical decision.

Supplementary Material

Figure 5 shows time-frequency plots separately for each LOI (i.e. LMOG in Fig. 5A and LIFGpo in Fig. 5B) and for each of the four experimental conditions. In each case the time-frequency data are first normalized per frequency in the passive window for the period -800 to -600ms and expressed as percentage signal change relative to baseline. These computations were made separately for each participant, site and condition. Then the normalized time-frequency plots were averaged across participants to create a grand averaged time-frequency plot for each case in Fig. 5.

Figure 5 about here



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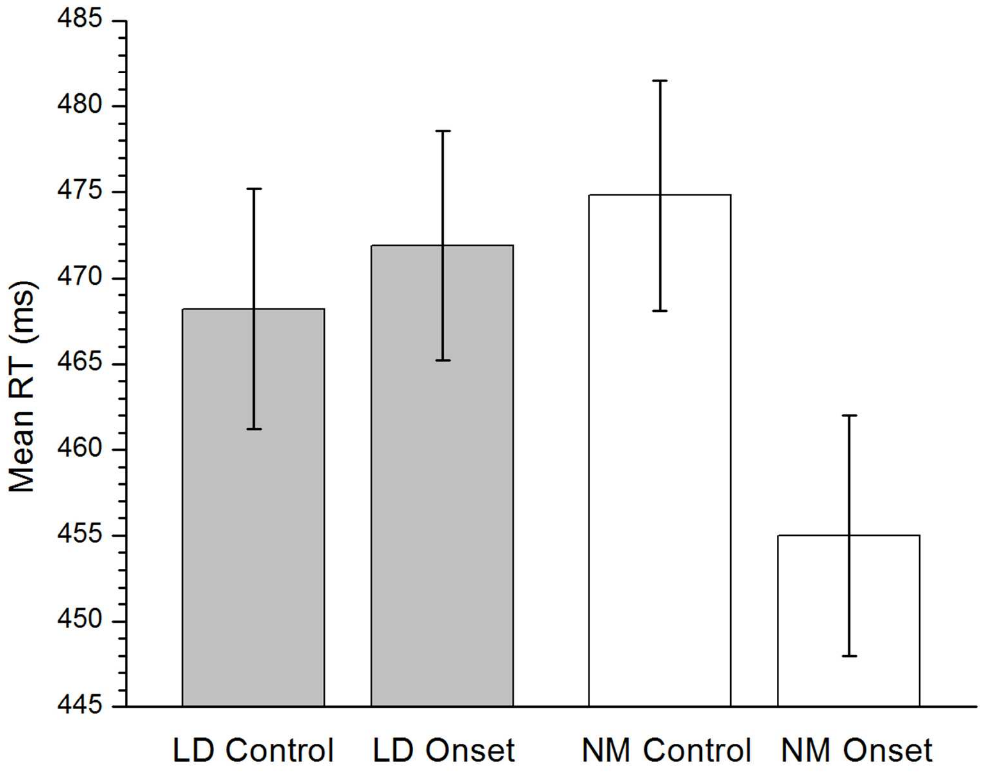

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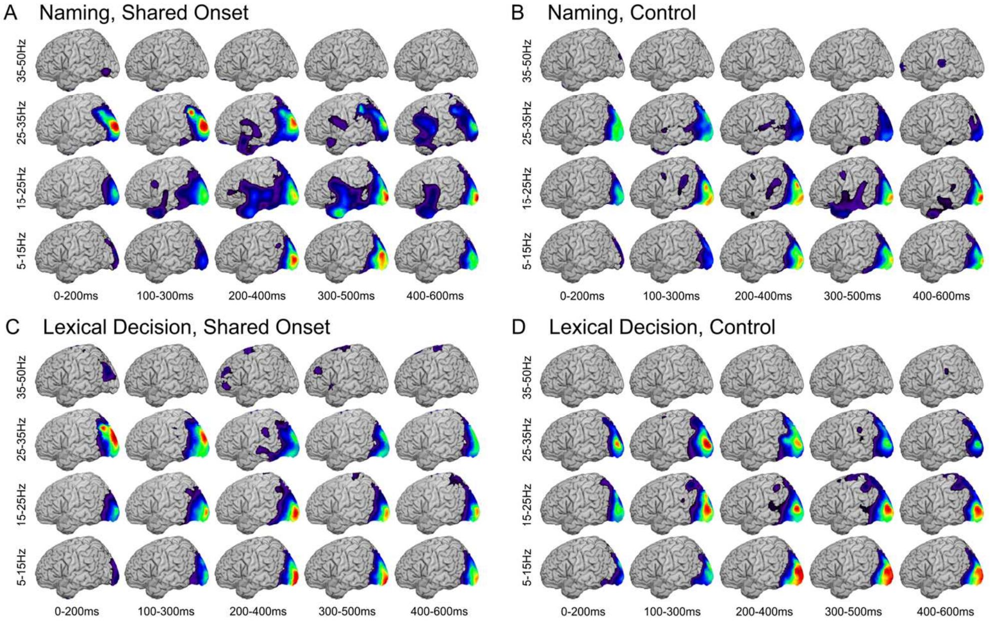

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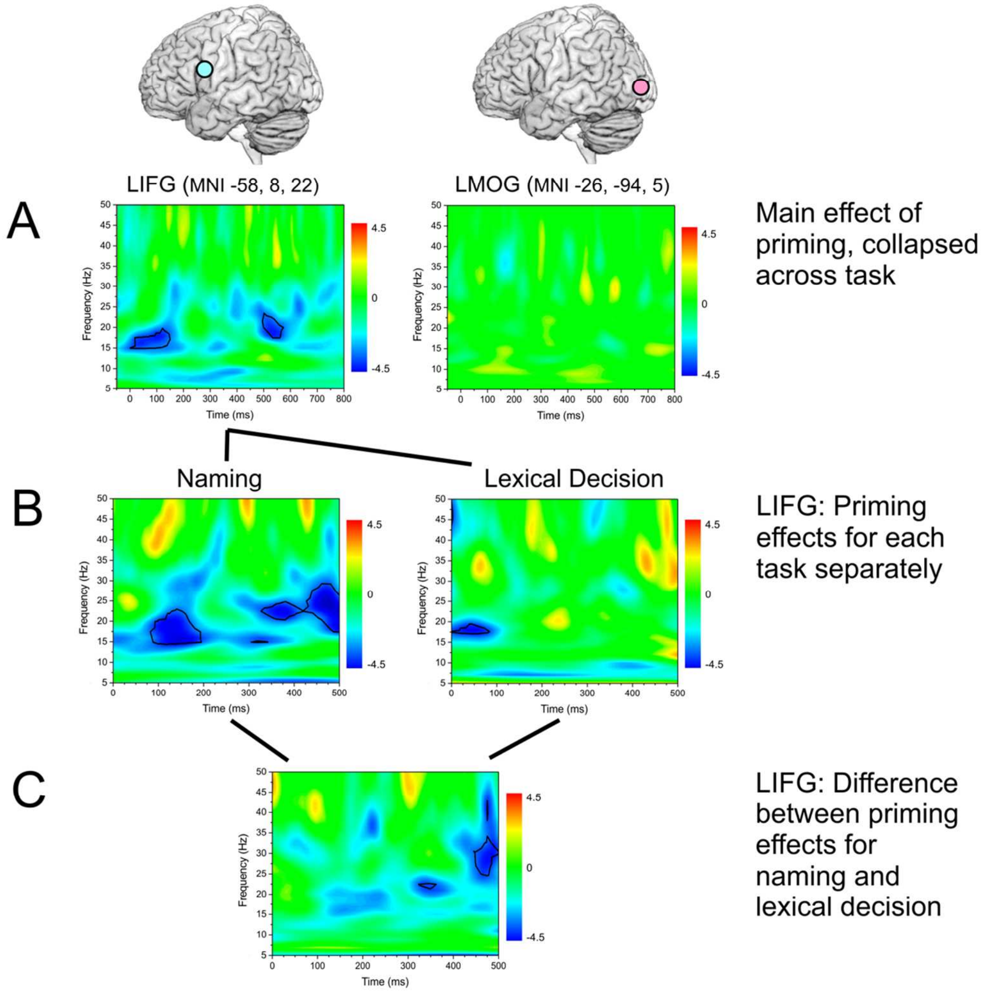

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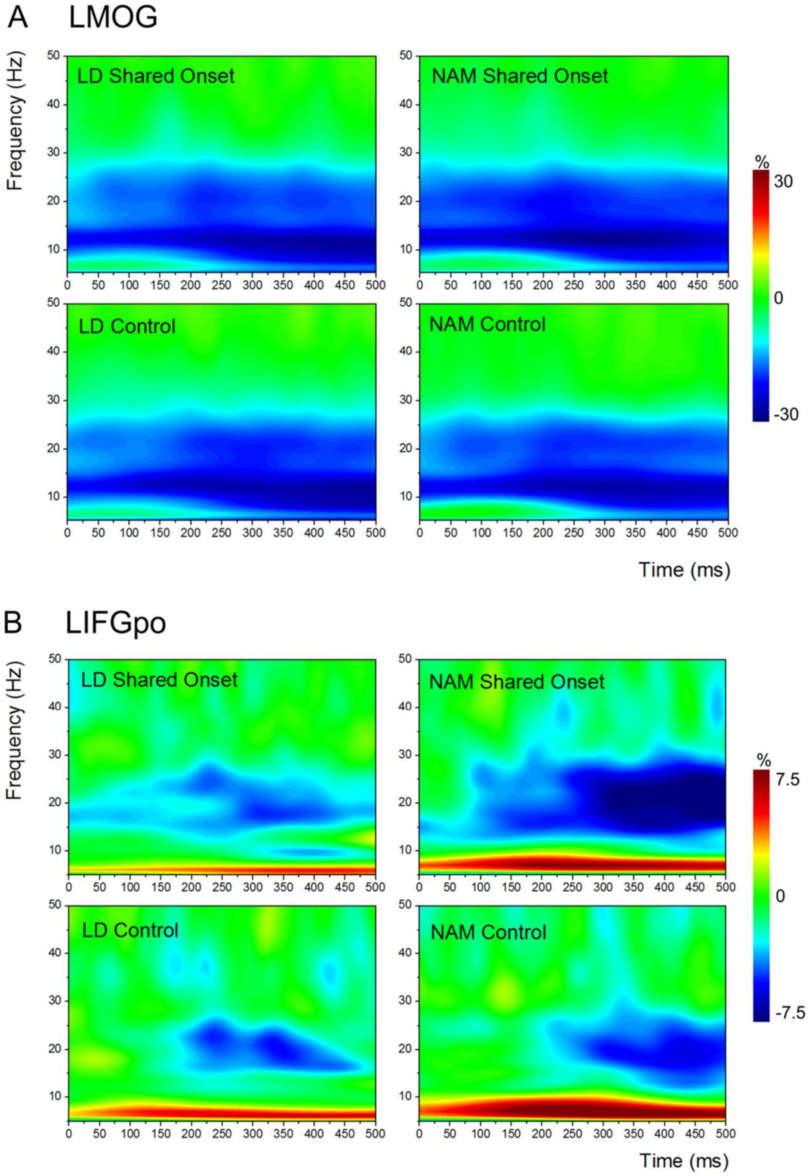

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