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The role of temporal predictability in semantic expectation: An MEG investigation

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ABSTRACT

Prior research suggests that prediction of semantic and syntactic information prior to the bottom-up input is an important component of language comprehension. Recent work in basic visual and auditory perception suggests that the ability to predict features of an upcoming stimulus is even more valuable when the exact timing of the stimulus presentation can also be predicted. However, it is unclear whether lexical-semantic predictions are similarly locked to a particular time, as previous studies of semantic predictability have used a predictable presentation rate. In the current study we vary the temporal predictability of target word presentation in the visual modality and examine the consequences for effects of semantic predictability on the event-related N400 response component, as measured with magnetoencephalography (MEG). Although we observe robust effects of semantic predictability on the N400 response, we find no evidence that these effects are larger in the presence of temporal predictability. These results suggest that, at least in the visual modality, lexical-semantic predictions may be maintained over a broad time-window, which could allow predictive facilitation to survive the presence of optional modifiers in natural language settings. The results also indicate that the mechanisms supporting predictive facilitation may vary in important ways across tasks and cognitive domains.

1. Introduction

Many decades of work in psycholinguistics has established that the broader context in which a word appears has a huge impact on the speed and accuracy of comprehension. More recent research suggests that a major means by which context affects language comprehension is through predictive processing, in which representations are activated or constructed in advance of the corresponding bottom-up input (DeLong, Urbach, & Kutas, 2005; Dikker, Rabagliati, & Pylkkänen, 2009; Federmeier, 2007; Lau, Phillips, & Poeppel, 2008; Van Petten & Luka, 2012; Wicha, Moreno, & Kutas, 2004). For example, given the context '*It was a windy day, so the boy went out to fly a...*', it has been proposed that the lexical and/or conceptual representation of '*kite*' will be 'preactivated' (e.g., Federmeier & Kutas, 1999) and that this representation will be

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prematurely added to a working memory representation of the sentence or message (e.g., Lau, Holcomb, & Kuperberg, 2013) in advance of the bottom-up input. Similarly, in the context of a series of highly related word pairs, one might strongly predict the word '*dog*' following the word '*cat*'.

At the same time, the details of the predictive mechanism utilized by the brain to facilitate on-line comprehension are still largely unknown. In the current study, we seek to gain insights into this mechanism by using magnetoencephalography (MEG) to examine the impact of *temporal* predictability on predictive semantic facilitation. In particular, given that comprehenders perceive natural speech as proceeding at a rhythmically regular and predictable rate in real-world comprehension contexts (Dilley, Wallace, & Heffner, 2012), we ask whether the processing gains accrued by the comprehender from having predicted the semantic content of a word are contingent on also having predicted *when* the word would appear.

Past behavioral studies have repeatedly demonstrated that a word is recognized faster when it is preceded by a semantically related word compared to a semantically unrelated word, a phenomenon known as semantic priming (see Neely, 1991, for review), and a similar reaction time benefit is observed for responses to words that appear in supportive sentence contexts (Fischler & Bloom, 1979; Stanovich & West, 1981). However, because behavioral studies usually measure responses to metalinguistic tasks and do not allow precise estimation of the timing of processes, in the current study we focus on a neural correlate of this contextual facilitation: the amplitude of the electrophysiological component known as the N400. The N400 is a broad peak between 300 and 500 msec in the event-related potential (ERP) associated with stimuli that carry meaning, such as words, pictures, and faces (Kutas & Federmeier, 2011). Critically, the amplitude of this peak has been observed to depend on the broader context, such that in many of the same paradigms in which processing facilitation is observed behaviorally (semantic priming, supportive sentence contexts), the amplitude of the N400 component is reduced (Kutas & Hillyard, 1980; 1984; Rugg, 1985).

Behavioral contextual facilitation and the neural modulation associated with it could reflect the result of predictive mechanisms, but it could also reflect more generic mechanisms such as bottom-up spreading activation between stored lexical-semantic representations. Several past findings suggest that the N400 can be modulated by prediction in particular. Federmeier and Kutas (1999) showed that the N400 was reduced in response to words that did *not* fit the sentence context as long as they shared semantic features with the word most strongly predicted by the context. More conclusively, elegant work by DeLong et al. (2005) demonstrated N400 modulation due to predictibility alone, when semantic association and bottom-up contextual congruity were tightly controlled.

In semantic priming paradigms, facilitation at short prime-target intervals (less than 200 msec) is believed to be due to automatic spreading activation, while facilitation at longer prime-target intervals is believed to be driven by 'controlled' mechanisms such as prediction. At long prime-target intervals, behavioral facilitation for semantically related pairs can be increased by increasing the number of related pairs in the experiment (e.g., 10% related trials versus 50% related trials), while relatedness proportion has little effect on the size of the priming effect at short prime-target intervals (e.g., de Groot, 1984; den Heyer, Briand, & Dannenbring, 1983; Hutchison, Neely, & Johnson, 2001; although cf. Bodner & Masson, 2003). This asymmetry can be accounted for by the idea that a higher proportion of related trials in the experiment will lead participants to generate stronger predictions for the target based on the prime, while leaving the automatic process of spreading activation unaffected. Correspondingly, electrophysiological experiments using the relatedness proportion paradigm suggest that N400 effects at long prime-target intervals largely reflect predictive facilitation, as the effect of relatedness on the N400 is quite small at low relatedness proportions and increases with higher relatedness proportion (e.g., Brown, Hagoort, & Chwilla, 2000; Holcomb, 1988; Lau, Holcomb et al., 2013; Lau, Weber, Gramfort, Hämäläinen, & Kuperberg, 2014). However, semantic priming at short prime-target intervals also modulates the N400 (e.g., Anderson & Holcomb, 1995; Lau, Gramfort, Hämäläinen, & Kuperberg, 2013), indicating that the N400 is also sensitive to facilitation due to bottom-up spreading activation. These findings can be reconciled according to a view in which N400 amplitude indexes the extent of lexical-semantic activation across the network, and in which both prediction and spreading activation act to preactivate the candidate representation such that activation is more narrowly focused when the critical word is presented (Lau et al., in press).

Although there is thus increasing evidence that predictive mechanisms underlie many semantic facilitation effects, the nature and timing of these mechanisms is still poorly understood. While bottom-up spreading activation has been thought to onset and decay rapidly, it is not so clear that this should be the case for preactivation due to predictive processes. On the one hand, predictive activation may need to extend across time to accommodate cases in which the exact moment of the predicted word's representation is not known, for example in the presence of optional modifiers (*… the boy went out to fly a new kite…*). Furthermore, lexical predictions may depend on higher-level linguistic information, and thus predictions may be delayed until these higher-level representations can be constructed (Chow, 2013).

On the other hand, it may be the case that in a naturalistic setting, the timing of a predicted word can in fact be accurately approximated most of the time. A little remarked-upon property of almost every previous study to examine semantic prediction is that stimulus presentation is fairly rhythmic. Experiments using auditory presentation contain the temporal regularities inherent in natural speech. Although prior work indicates that syllables of perceptually natural speech are not produced at an objectively constant rate (e.g., Fowler, 1979; Hoequist, 1983; Morton, Marcus, & Frankish, 1976), comprehenders have strong intuitions about the timing which results in perceived isochrony, and appear to use this to predict syllable onsets and facilitate speech perception (Dilley et al., 2012). Experiments using visual presentation typically implement a constant stimulus onset asynchrony (SOA) throughout an experimental block of trials. Such temporal regularity makes it possible for listeners or readers to predict approximately when the next word will be presented.

Previous research across multiple cognitive domains has demonstrated that temporal predictability has reliable impacts on both behavioral responses and neural activity, for example in both visual and auditory perception (e.g., Doherty, Rao, Mesulam, & Nobre, 2005; Jones, Moynihan, MacKenzie, & Puente, 2002; see Näätänen & Picton, 1987 for an early review of auditory work and Nobre, Correa, & Coull, 2007 for a more recent cross-domain review). Of note here, a number of studies indicate that such temporal predictions interact synergistically with other kinds of predictive information (e.g., Costa-Faidella, Baldeweg, Grimm, & Escera, 2011; Doherty et al., 2005; Hsu, Hämäläinen, & Waszak, 2013; Kingstone, 1992; Rohenkohl, Gould, Pessoa, & Nobre, 2014). For example, Rohenkohl et al. (2014) showed that temporal predictability improves performance on a visual discrimination task if participants know ahead of time where the target is likely to appear, but it has no effect in the absence of this kind of spatial expectation. Similarly, Doherty et al. (2005) found that temporal expectation only modulated the P1 attentional component in the presence of spatial expectations. Although less well-studied, there is some evidence that non-spatial predictions for visual features also interact with temporal predictions to facilitate behavioral responses (Kingstone, 1992).

The mechanism by which temporal predictability exerts these effects is only beginning to be understood. Recent work has suggested that temporal expectation facilitates perceptual rather than decision-level processing (Jepma, Wagenmakers, & Nieuwenhuis, 2012; Rohenkohl, Cravo, Wyart, & Nobre, 2012). For example, Rohenkohl et al. (2012) show temporal expectation impacting visual perception by increasing the effective contrast of the visual stimulus. It has been widely suggested that such a mechanism could be implemented through modulation of ongoing oscillations in neural firing: oscillatory activity in relevant neural populations becomes entrained to a regular stimulus rate, or a stimulus event acts as a trigger to reset the phase of the oscillations, so that the relevant neurons for the predicted stimulus are in the optimal state to react when the stimulus is presented (e.g., Arnal & Giraud, 2012; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008; Stefanics et al., 2010).

The goal of the current work was to begin to investigate how exactly linguistic predictions are impacted by temporal predictability. If semantic prediction were implemented through an oscillatory signal phase-locked to stimulus presentation, pre-activation would be relatively brief and targeted to the particular time-window in which the expected word was likely to be presented. Conversely, tying lexical-semantic predictions to a narrow time-window may be non-optimal because of the availability of optional modifiers and alternative syntactic frames in natural language contexts. Here, we investigate these possibilities by examining how temporal expectation interacts with the well-established effect of semantic expectation on the N400 response to visual words in a semantic priming paradigm. Following previous work, we manipulate temporal predictability by varying the regularity of stimulus onset asynchrony times (Costa-Faidella et al., 2011; Schwartze, Farrugia, & Kotz, 2013). We use visual presentation because it allows tighter control of the onset of semantic information (the entire word is presented instantaneously, rather than being spread across time) and because randomized temporal irregularity is less jarring in the more artificial rapid serial visual presentation paradigm than it would be in otherwise naturalistic speech. We use MEG to record the N400 response rather than EEG because MEG responses are more focal than EEG, allowing us to focus on sensors corresponding to the left-hemisphere neural populations that give rise to the largest N400 effect (Lau, Almeida, Hines, & Poeppel, 2009; Lau et al., 2008). We also conduct distributed source localization analyses to confirm the standard left anterior temporal location for our semantic predictability effects and to better account for individual differences in head position.

2. Material and methods

2.1. Materials

As visually summarized in Table 1, the stimulus materials were comprised of 448 prime-target pairs, arranged in a 2 × 2 design (temporal predictability: predictable/unpredictable × semantic predictability: predictable/unpredictable). In a given session there were 4 blocks in the temporally predictable set and 4 in the temporally unpredictable set. In the temporally predictable set, each block had a consistent stimulus-onset asynchrony (SOA) between the onset of the prime and target of each word pair. In the temporally unpredictable set, the SOA between the onset of the prime and target of each word pair was always variable. Each experimental block had an equal number of semantically predictable (related) and semantically unpredictable (unrelated) pairs, distributed equally across 4 SOAs (200, 400, 600, 800 msec) in temporally unpredictable blocks. As these same 4 SOAs were used in the

Table 1 – Distribution of stimuli broken down by temporal predictability, semantic predictability, and stimulus-onset asynchrony (SOA), across the 8 blocks.

	Temporally unpredictable	Temporally predictable
1	200 msec/400 msec/600 msec/800 msec: 7 related, 7 unrelated for each SOA	200 msec: 28 related, 28 unrelated
2	200 msec/400 msec/600 msec/800 msec: 7 related, 7 unrelated for each SOA	400 msec: 28 related, 28 unrelated
3	200 msec/400 msec/600 msec/800 msec: 7 related, 7 unrelated for each SOA	600 msec: 28 related, 28 unrelated
4	200 msec/400 msec/600 msec/800 msec: 7 related, 7 unrelated for each SOA	800 msec: 28 related, 28 unrelated

temporally predictable blocks, this design allowed us to compare overall effects of temporal and semantic predictability without introducing temporal onset confounds in the evoked responses. Our shortest lag of 200 msec is at the boundary of the minimum amount of time thought to be required for generating lexical-semantic predictions in the semantic priming paradigm (Neely, 1991). Therefore, it is possible that semantic predictability effects would be larger at the longer SOAs, independent of temporal predictability, and we investigated this possibility by including SOA as a factor in our analysis.

The word pair stimuli were adapted from a previous study (Lau, Holcomb et al., 2013). To create the lists of related and unrelated pairs, 448 highly associated prime-target pairs were selected from the University of South Florida Association Norms (Nelson, McAvoy, & Schrieber, 2004) with the selection criteria being a forward association strength of .4 or higher. A forward association strength of .4 signifies that at least 40% of participants, out of at least 100 participants presented with the prime word in a free association task, responded with the target word. The mean log frequency of the prime and targets used were 2.54 and 3.51, respectively, as computed in the SUBTLEXus (Brysbaert & New, 2009). Pairs with morphological overlap between prime and target were excluded to minimize effects of morphological similarity. Pairs with function words were also excluded because, relative to content words, function words have been observed to elicit smaller N400 responses (Kutas & Hillyard, 1983; Münte et al., 2001; Van Petten & Kutas, 1991) To prevent item-specific effects, no words were repeated within the study.

The 448 related pairs were divided into two sets such that forward probability was roughly matched across sets. Within each set, half of the stimuli were kept intact as related pairs, and half were formed into unrelated pairs by randomly redistributing the primes across the target items and manually checking for accidental associations. The list of stimuli presented to each participant was individualized (with 8 lists repeated), such that forward probability was roughly matched across jittered and constant conditions, and across SOAs. In total, 16 different participant lists were created.

Each list was composed as follows. In the temporally predictable condition, each of the 4 blocks had a consistent SOA of either 200, 400, 600, or 800 msec between the onsets of the prime and target words, with 28 unrelated and 28 related word pairs. In the temporally unpredictable condition, each block consisted of a presentation of 14 word pair trials with an SOA of 200 msec, 14 of 400 msec, 14 of 600 msec, and 14 of 800 msec, with 7 related and 7 unrelated trials for each SOA, making up a total of 28 unrelated and 28 related trials within each block. Each block was preceded by a random presentation of 4 related and 4 unrelated filler trials following the timing parameters of that block in order to help participants identify and adapt to the rhythm, or lack thereof.

2.2. *Distractor task*

In order to encourage attention to the stimuli, participants were asked to perform a memory test at the conclusion of each block. During the memory test, participants were presented one word at a time, and were asked to respond indicating whether or not they had encountered the word in the previous block. Participants were tested with 10 words for each block (5 old and 5 new), and were provided with immediate feedback after each response. The memory task was self-paced.

2.3. *Stimulus presentation*

Participants were assigned one of 16 stimulus lists, which incorporated counterbalancing for presentation orders (temporally predictable followed by unpredictable or vice versa). Stimuli were visually presented on a projector screen above the participant in white 20-point uppercase Arial font on a black background. The visual angle subtended by the critical words was approximately 1°.

In order to maintain the same total duration for each block across SOA conditions, we varied both the stimulus-onset asynchrony and the duration of the target, such that each trial had the same total length. While this allowed us to hold trial duration constant across conditions, this design could raise the concern that conditions in which the target duration was shorter or variable would be processed less deeply. The primary reason we do not believe this is likely to occur is that the shortest target duration, at 800 msec, is quite long relative to the latency of the component of interest (350–450 msec) and relative to the duration of a typical word in speech or of a fixation in reading. This concern might also predict that accuracy on the memory paradigm would be worse for temporally variable blocks, which as we report below, was not the case.

Each trial began with a fixation cross presented at the center of the screen for 1000 msec, followed by a 100 msec blank screen. The prime word was then presented for 150 msec, followed by a blank screen for 50, 250, 450, or 650 msec depending on the SOA condition. Correspondingly, the target word was presented for 1400, 1200, 1000, or 800 msec, followed by a 100 msec blank screen prior to the onset of the next trial. In total, each trial lasted for 2800 msec (see Table 2 and Fig. 1). The 4 blocks within each condition set were presented in a random order, followed by the memory test and a self-paced break for participants to rest their eyes. There was a mandatory one-minute break after the 4th block

Table 2 – Timing of events in a trial, for the 4 stimulus-onset asynchrony (SOA) conditions used in the experiment.

Fixation duration	Blank duration	Prime duration	ISI duration	SOA (prime + ISI)	Target duration	Blank duration
1000 msec	100 msec	150 msec	50 msec	200 msec	1400 msec	100 msec
			250 msec	400 msec	1200 msec	
			450 msec	600 msec	1000 msec	
			650 msec	800 msec	800 msec	

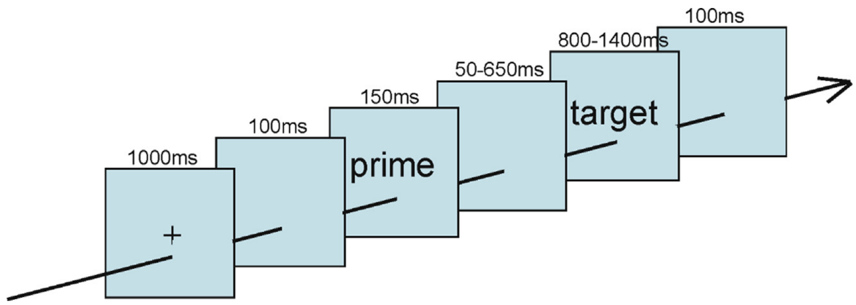

Fig. 1 – Illustration of the stimulus presentation sequence used for each trial in the experiment.

memory test, marking the halfway point and separating the two conditions.

2.4. Participants

Participants were recruited from the University of Maryland, College Park community. Data presented here is from 24 participants (8 men and 16 women) aged 18–28 years (mean = 21.2 years) who met the constraints below and who had a minimum of 16 trials (out of 28) for each SOA category in both temporal predictability conditions (given the 4 SOAs, this ensured at least 64 trials for each cell of the temporal × spatial predictability design). All participants were right-handed (Oldfield, 1971) native speakers of American English who had not learned another language before the age of 5 years, with normal or corrected to normal vision and no history of reading disabilities or neurological disorders. Written informed consent was obtained for all participants prior to the experimental session. Participants were compensated at a rate of $10/h.

2.5. MEG recording and analysis

Prior to recording, five head position indicator coils were affixed to each participant's head, and the position of these coils relative to the nasion and tragus, as well as the participant's headshape, was digitized using a Polhemus 3SPACE FASTRAK system in order to determine the participant's accurate placement in the MEG dewar. During the experimental sessions, participants laid supine in a dimly lit magnetically shielded room (Yokogawa Industries, Tokyo, Japan). Continuous MEG recording was executed using a 160-channel axial gradiometer whole-head system (Kanazawa Institute of Technology, Kanazawa, Japan), and data was sampled at 500 Hz (60 Hz online notch filter, DC-200 Hz recording bandwidth).

A time-shift PCA filter (De Cheveigné & Simon, 2007) was applied to the continuous MEG data offline in order to remove external sources of noise artifacts. Using the MNE software package (www.martinos.org/mne), averaged event-related MEG signals time-locked to target words were computed offline, from trials free of ocular and muscular artifacts in the time-window from 100 msec pre-stimulus to 600 msec post-stimulus. Artifact rejection resulted in the loss of 7.7% of all trials. A 20 Hz low-pass filter only was applied and the 100 msec pre-stimulus baseline was subtracted from all waveforms prior to statistical analysis.

Both sensor and source analyses focused on the 350–450 msec time window post-target word onset, at which the N400 context effect is typically at its peak. The goal of the study was to determine what effect temporal prediction would have on the size of the N400 semantic predictability effect. Therefore, we constrained our sensor analyses to those MEG sensors that showed the most robust N400 effect across all conditions. Previous MEG work has demonstrated that N400 contextual facilitation effects are strongest in the left hemisphere, in the form of a magnetic dipole with a magnetic sink over anterior sensors and a source over posterior sensors (Halgren et al., 2002; Helenius, Salmelin, & Connolly, 1998; Lau et al., 2009; Lau, Gramfort et al., 2013; Lau et al., in press; Uusvuori, Parviainen, Inkinen, & Salmelin, 2008). Therefore, we computed a grand-average difference map across participants illustrating the mean activity for semantically unpredictable – semantically predictable targets in the 350–450 msec time-window collapsed across all conditions, and selected 15 sensors in the left anterior sink and 15 sensors in the left posterior source that showed the largest differences. We then used activity from these selected sensors to compute a 2 × 2 × 4 repeated-measures ANOVAs (semantic predictability × temporal predictability × SOA) in the left anterior region and the left posterior region. As stimulus-onset asynchrony should have a main effect on responses for uninteresting reasons (i.e., the degree to which the evoked response to the prime overlaps that of the target) here we report only effects that involve interactions with semantic predictability or temporal predictability.

For the source analyses, the MNE software package (Gramfort et al., 2014) was used to derive source estimates on the cortical surface for MEG responses in each participant. The ‘fsaverage’ template brain from the FreeSurfer software package (http://surfer.nmr.mgh.harvard.edu) was used as an approximation for individual anatomy, and digitizer data was used to manually coregister individual head position to the template brain. A three-compartment boundary element model computed for this template brain with the linear collocation approach was used in the forward calculation (Hämäläinen & Sarvas, 1989; Mosher, Leahy, & Lewis, 1999). The amplitudes of the dipoles at each cortical location were estimated for each time sample using the anatomically-constrained linear estimation approach (Dale et al., 2000).

Noise covariance estimates were derived from data recorded in the 100 msec baseline period prior to the presentation of the prime word for all trials. The orientations of the dipoles were approximately constrained to the cortical normal direction by reducing the variance of the source components tangential to the cortical surface by a factor of .2 (Lin, Belliveau, Dale, & Hämäläinen, 2006). We computed dSPM source estimates of activity at the cortical surface for the −100 msec pre-stimulus to 600 msec post-stimulus epochs described above, for each participant for all 16 conditions. Individual estimates were smoothed using 7 iterative steps to spread estimated activity to neighboring vertices. For visual examination, a grand-average dSPM contrast map was created by subtracting the semantically predictable from unpredictable activity estimates (unpredictable − predictable) across all vertices, averaging across participants, and then averaging the estimates across the 350–450 msec time-window. This difference map was used to identify the left anterior temporal region where the semantic predictability N400 effect was at its maximum. We then extracted mean source estimates from this region in the 350–450 msec time-window for each participant and condition, and computed a 2 × 2 × 4 repeated-measures ANOVA (semantic predictability × temporal predictability × SOA) on these data. As in the sensor analyses, we report only effects that involve interactions with semantic predictability or temporal predictability.

3. Results

3.1. *Sensor analysis*

Mean accuracy on the memory tests was 69% for temporally predictable blocks and 69% for temporally unpredictable blocks. Visual inspection of the MEG evoked responses to semantically predictable and unpredictable targets, collapsed across temporal predictability and SOA, revealed a robust effect of semantic predictability in the 350–450 msec time-window (Fig. 2). Replicating previous work, this effect was reflected as a strong anterior sink – posterior source pattern in the left hemisphere, consistent with a generator in temporal cortex, and a more asymmetric pattern in the right hemisphere with a stronger effect over anterior sensors (Lau et al., 2009). In order to confirm the presence of an N400 semantic predictability effect prior to region-of-interest analyses, we conducted simple paired sample *t*-tests contrasting related versus unrelated responses in the 350–450 msec time-window in each of four independently defined sensor quadrants (27 sensors in each). These tests revealed significant effects of semantic predictability in left anterior [$t(23) = 4.36$, $p < .01$], left posterior [$t(23) = 2.51$, $p < .05$], and right anterior [$t(23) = 2.16$, $p < .05$] quadrants.

Fig. 3 illustrates responses to semantically predictable and unpredictable targets separately for temporally predictable and unpredictable conditions, in the subset of left anterior and left posterior sensors selected for further analysis. While differences in the size of the semantic predictability effect were visually apparent in the left posterior region, surprisingly this took the form of a larger semantic predictability effect for the temporally unpredictable condition. This pattern was confirmed by statistical analyses: while the left anterior region demonstrated no significant effects beyond the expected main effect of semantic predictability (not meaningful, given that the sensors were selected on the basis of the size of this effect), the left posterior region additionally demonstrated a significant interaction between semantic and temporal predictability [$F(1,23) = 6.39$, $p < .05$]. The fact that effects in the anterior and posterior quadrant did not fully track each other, as would be expected if they simply reflected the sink and source of a single magnetic dipole, suggests that activity from other non-shared sources may have been overlaid on these sensors during the N400 time-window.

No other significant interactions were observed. In particular, although there was some numerical variability in the size of the semantic predictability effect at each level of temporal predictability across SOAs (Fig. 4), neither the interaction between SOA and semantic predictability nor the three-way interaction between SOA, semantic predictability, and temporal predictability were significant in either quadrant ($ps > .15$).

Finally, visual inspection of the MEG data indicated a possible interaction between temporal predictability and semantic predictability over left anterior sensors in a much earlier time-window, between 100 and 150 msec. Because previous investigators have reported interactions between temporal predictability and spatial predictability on the P1 component (Doherty et al., 2005), we investigated this interaction further by conducting an exploratory repeated measures ANOVA in the left anterior region in the 100–150 msec time-window. Although the results of this post-hoc analysis should be taken as suggestive only, we did observe a significant interaction between semantic and temporal predictability [$F(1,23) = 10.1$, $p < .01$].

3.2. *Source analysis*

The grand-average distributed source space map illustrating the difference between the response to semantically unpredictable and predictable words between 350 and 450 msec is provided in Fig. 5. As in previous work (Lau, Gramfort et al., 2013; Lau et al., in press), we observed reduced activity for semantically predictable words relative to unpredictable words in left anterior temporal cortex. The current locus of this effect was somewhat anterior to what was reported in the previous work, which is likely due to the fact that in the current study we coregistered the participants' MEG data to a template brain rather than individual anatomical scans, introducing some potential inaccuracy in the exact localization.

As in the sensor-space analysis, the main effect of semantic predictability was used to guide follow-up analyses. Taking this left anterior temporal region as our region-of-interest, we extracted the mean estimated source amplitude across this region in the 350–450 msec time-window for each participant and condition, and entered these data into a repeated measures ANOVA (semantic predictability × temporal predictability × SOA). Again the results showed no significant main effects or interactions involving semantic predictability or temporal predictability, beyond the main effect of semantic predictability (not meaningful, given that the

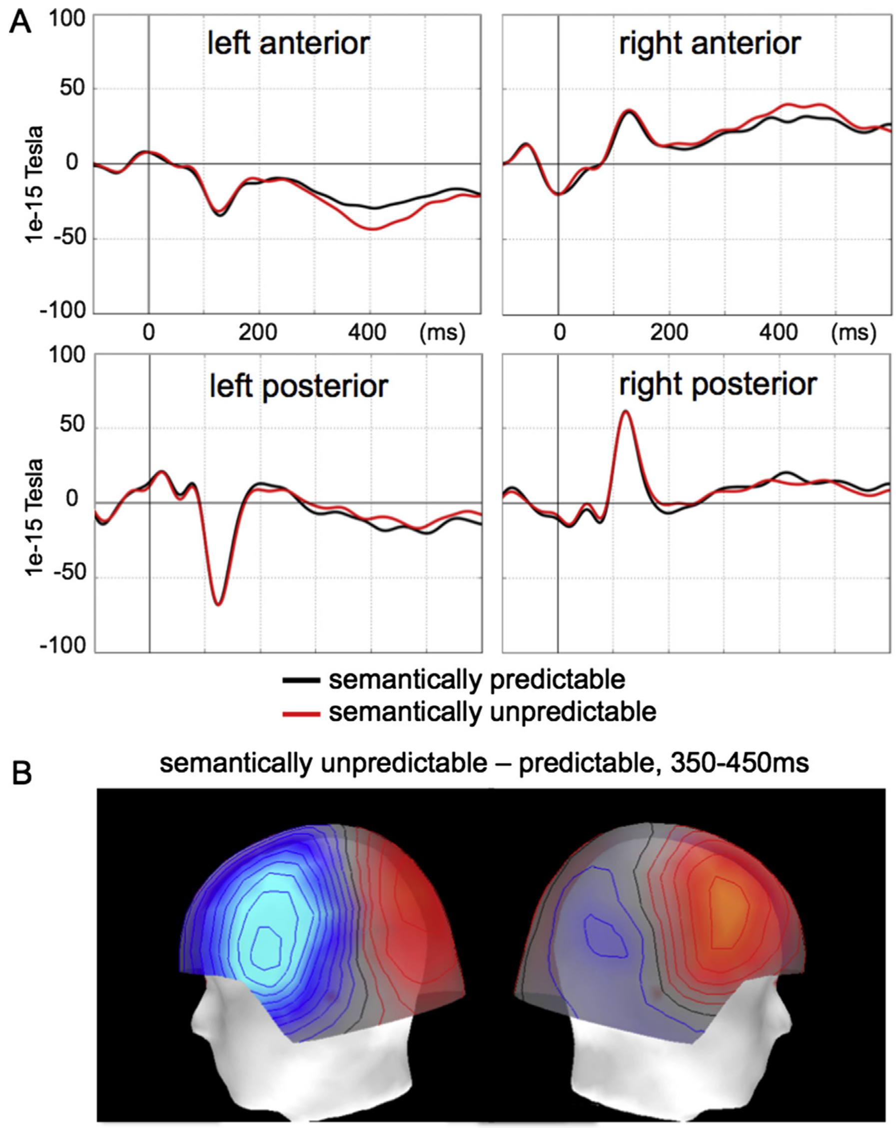

Fig. 2 – Mean responses to semantically predictable and unpredictable items, collapsed across temporal predictability. A. Grand-average magnetic field strength in response to target words, averaged across 27 sensors in each of four independently-defined sensor quadrants. B. Topographic magnetic field map displaying the mean difference between semantically unpredictable and predictable responses across the 350–450 msec time-window.

region was selected on the basis of this effect). In particular, there was no hint of an interaction between semantic predictability and temporal predictability ($F < .1$), and the effect of semantic predictability was almost identical across levels of temporal predictability (Fig. 5). These data suggest that the reverse interaction observed between semantic and temporal predictability in the left posterior sensor analysis may have been due to a source other than the one responsible for standard semantic predictability N400 effects.

4. Discussion

The goal of the current study was to investigate the hypothesis that temporal predictability might play an important role in the semantic predictability effects indexed by the N400 effect; in other words, that a reasonably good estimate of *when* a word will appear might be necessary in order to fully benefit from contextual clues about *what* the word will be. The current results suggest that this hypothesis is not borne out in visual word presentation. We observed no hint of an interaction between semantic and temporal predictability in the MEG source localization analysis or in the sensor analysis in the left anterior sensors that showed the strongest main effect of semantic predictability, and to the extent that we observed any interaction between semantic predictability and temporal predictability it went in the opposite direction, such that the effect of semantic predictability was significantly larger in left posterior sensors for the jittered-SOA condition in which the timing of target presentation was highly uncertain.

We take these results to suggest that the mechanism supporting facilitation due to semantic prediction does not

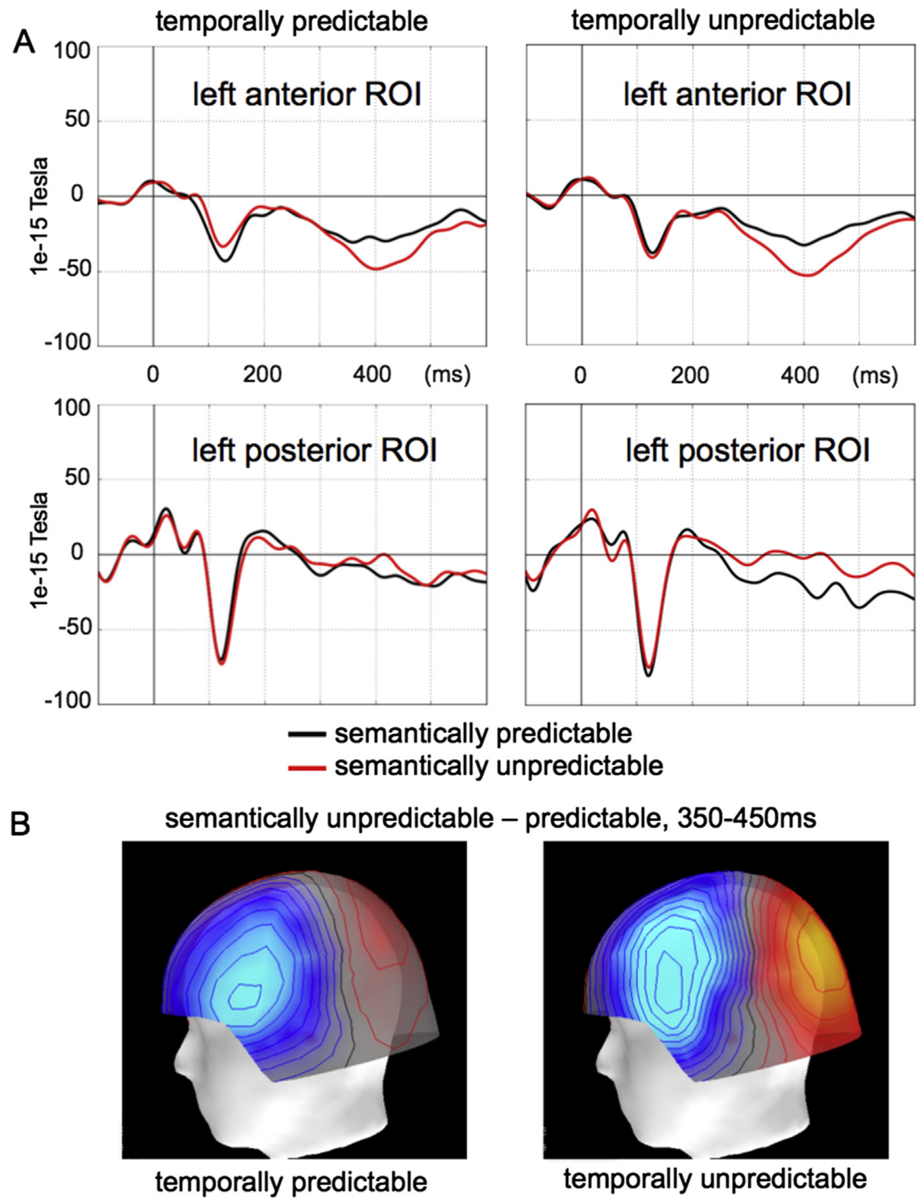

Fig. 3 – Mean responses to semantically predictable and unpredictable items across selected left hemisphere sensors at each level of temporal predictability. A. Grand-average magnetic field strength in response to target words, averaged across 15 left anterior sensors and 15 left posterior sensors demonstrating a robust main effect of semantic predictability. B. Topographic magnetic field maps displaying the mean difference between semantically unpredictable and predictable responses across the 350–450 msec time-window in the left hemisphere.

depend on a precise estimate of the time at which a word will appear. As noted in the introduction, interactions between spatial and temporal predictability have been reported in visuospatial tasks, and these results thus suggest the existence of interesting differences in how predictions are implemented across modalities and cognitive domains. In the visuospatial domain, predictions about where a stimulus will appear next may be implemented through an attentional mechanism that is temporally specific; for example, according to oscillatory 'readiness' accounts, neural firing patterns could be reset such that visual units coding for the upcoming spatial location will be ready to fire at just the moment that the stimulus appears, improving the gain function (Arnal & Giraud, 2012; Lakatos & Schroeder, 2008; Rohenkohl & Nobre, 2011; Stefanics et al., 2010). In contrast, the current findings support the idea that semantic predictions, rather than improving the gain of particular representational units, result in the preactivation of representational units that may be sustained across a longer timeframe. If the N400 response reflects the summed activity across multiple competing lexical-semantic representations (Laszlo & Plaut, 2012), then the mechanism by which predictions facilitate processing and reduce N400 amplitude may be to give the predicted representation a 'head-start' in activation, such that the competition is won before the rest of the network has time to be engaged. If the N400 response instead simply indexes the amount of semantic prediction error, as

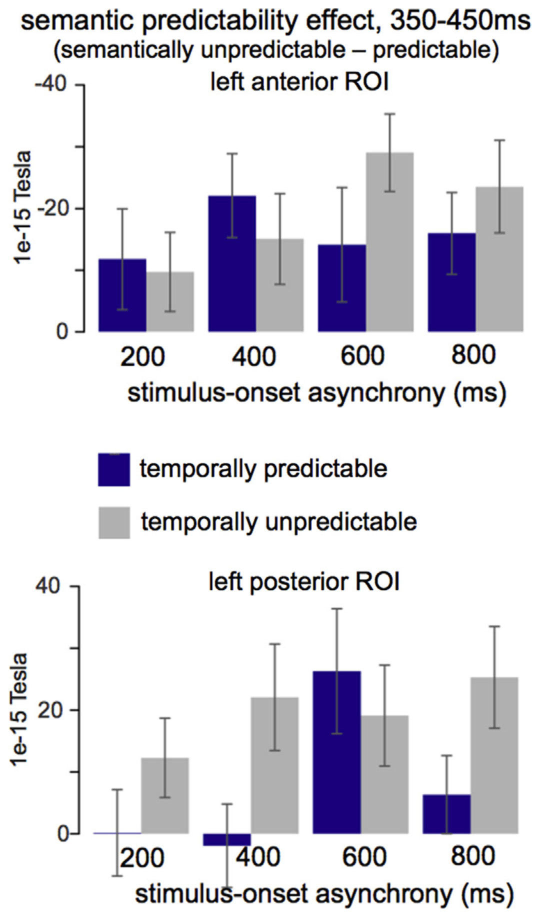

Fig. 4 — Semantic predictability effect (mean difference between semantically unpredictable and predictable responses) between 350 and 450 msec, displayed for left anterior ROI and left posterior ROI sensors, for each level of temporal predictability and stimulus-onset asynchrony. Error bars indicate standard error for each condition.

recently argued by Rabovsky and McRae (2014), the current findings suggest that the predictions that are compared with the input to compute prediction error must be sustained over time. One interesting open question regards exactly how long semantic preactivation is sustained in the presence of temporal uncertainty. In the current study, we demonstrated that semantic facilitation was robust to temporal variability in the range between 200 and 800 msec; it will be interesting for future work to explore whether this is the case over broader ranges spanning several seconds.

An alternative explanation for the lack of a facilitatory interaction between temporal and semantic predictability on the N400 is that the semantic priming paradigm used here does not elicit the same kinds of semantic or temporal predictions as more naturalistic language comprehension settings. We believe that this concern is more likely to hold for temporal prediction than semantic prediction. As reviewed in the introduction, previous behavioral and ERP studies using the relatedness proportion paradigm strongly suggest that predictive processes are a major contributor to the facilitation observed in semantic priming, especially when the prime and the target are separated by a reasonably long interval (Neely, 1991). More specifically, Lau, Holcomb et al. (2013) found a large predictive contribution to N400 facilitation in EEG using a stimulus onset-asynchrony of 600 msec, and in the current study the absence of the expected interaction between temporal and semantic predictability was especially clear for the 600 msec and 800 msec lags. Lau and colleagues also noted that the topographic distribution of the predictive N400 effect for semantic priming was identical to that observed in more naturalistic sentence paradigms (see Lau et al., 2009 for similar arguments based on less-distorted magnetic field distributions). These data suggest that word pair paradigms do induce semantic prediction.

On the other hand, many aspects of the timing of the current paradigm are very different from naturalistic speech, in ways that could lead to important differences in temporal prediction. For example, in our 'temporally predictable' conditions, we used a constant stimulus onset asynchrony between the first and second word to allow prediction of the onset, but in perceptually isochronous natural speech, words do not actually onset at a constant rate (Morton et al., 1976), and therefore comprehenders may not be accustomed to using true isochrony across trials to generate temporal predictions. Therefore it is possible that if the current experiment were repeated with naturalistic, perceptually isochronous speech stimuli were used, an interaction between semantic and temporal predictability would in fact be observed. Relatedly, in speech, where words are not presented instantaneously but are spread out across time, the most useful quantity to predict may not be absolute timing of word onset. For example, Rothermich, Schmidt-Kassow, and Kotz (2012) demonstrate that not temporal but metrical predictability (the ability to predict the position of a stressed syllable from the context) does interact significantly with semantic predictability, such that semantically unexpected words elicit a smaller N400 response in a metrically regular context compared to a metrically irregular context. They argue that predicting the position of stressed syllables may be especially important for optimizing speech perception, as this is when the perceptual input is maximally salient. Finally, in speech the contextual window over which temporal regularity is established can be many words long, allowing the potential for entrainment to the stimulus stream, whereas in the current study the stimuli were not presented in a continuous stream but were broken up into two-word trials. For these reasons, we believe it will be important to follow up our initial results with studies that manipulate timing using more naturalistic speech stimuli, in order to determine whether the current pattern of results extend to these cases, and if so, to better understand why.

One surprising aspect of the findings here was the observation of an interaction in the left posterior temporal quadrant opposite from what might have been expected, that is, that semantic predictability actually had a slightly larger effect on N400 amplitude when the temporal lag was unpredictable. One possible explanation is that the lack of temporal predictability led participants to be slightly more attentive overall during these blocks, such that the primes were processed more deeply, driving stronger or more accurate predictions of the target. At least one recent auditory study

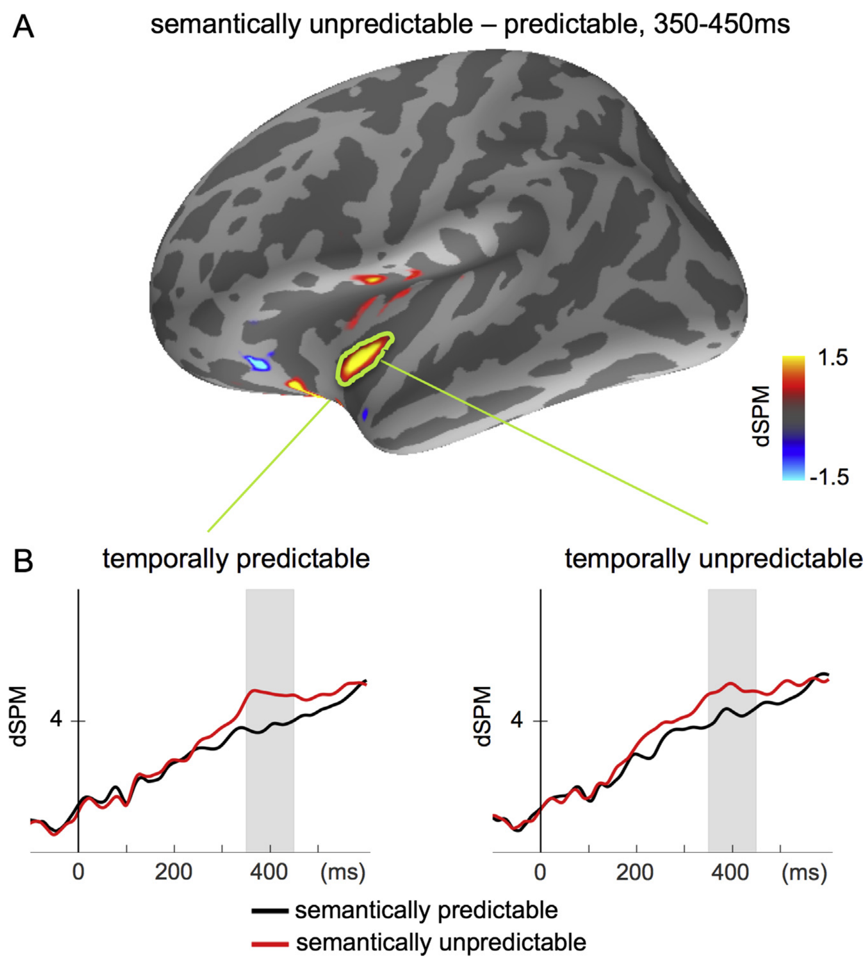

Fig. 5 – MNE distributed source estimates. A. Grand average difference map displaying the mean difference between semantically unpredictable and predictable dSPM source estimates between 350 and 450 msec, across participants. B. Waveform plots illustrating the mean dSPM activity estimates for the left anterior temporal region of interest at each level of semantic and temporal predictability.

(Schwartze et al., 2013) similarly showed a larger effect of predicting 'what' under temporally unpredictable conditions, in which the difference in the N1 response to an oddball tone versus the standard was larger when the tone stream was temporally irregular, and this interaction appeared to be more robust under attentive versus pre-attentive conditions. However, we note that behavioral accuracy on the memory task did not differ between temporally predictable and unpredictable blocks, as might be expected if participants were more attentive during the unpredictable blocks.

Unexpectedly, we also observed suggestive evidence of an interaction between semantic and temporal predictability in the much earlier P1 time-window. While in the temporally unpredictable conditions there was no difference between semantically predictable and unpredictable responses, in the temporally predictable conditions a negative peak over left anterior sensors was larger for semantically predictable than unpredictable targets, and an exploratory, post-hoc analysis found a significant interaction between semantic and temporal predictability between 100 and 150 msec. On the one hand, this effect appears consistent with Doherty et al.'s (2005) observation in the visual domain that the P1 response in EEG was largest in the presence of both spatial and temporal predictability. On the other hand, in the lexical-semantic domain such an early effect of semantic predictability would require either that lexical-semantic activation occur very early or that the lexical-semantic prediction were translated into a visual prediction (e.g., Dikker et al., 2009; Hauk, Davis, Ford, Pulvermüller, & Marslen-Wilson, 2006; Kim & Lai, 2012; Sereno, Rayner, & Posner, 1998). Although the idea that temporal predictability might interact with one of these early processes is intriguing, we await further replication before drawing strong conclusions because we did not predict the timing or location of this interaction.

One final caveat that should be noted regarding the current results is that because of our desire to record neurophysiological responses to the stimuli in the absence of explicit behavioral responses, we were not able to measure behavioral facilitation due to temporal and semantic predictability. It is possible that despite the absence of an interaction in N400 amplitude, temporal predictability would interact with semantic predictability in its impact on reaction times or accuracy; although in the visuospatial domain Doherty et al. (2005) failed to observe such an interaction in reaction times, Rohenkohl et al. (2014) observed a significant interaction in accuracy on a demanding psychophysical orientation detection task. N400 amplitude often correlates with reaction times and accuracy on tasks like lexical decision, but not always (Holcomb, 1993). Future work is therefore needed to explore this possibility.

Finally, although not the focus of the current investigation, these results provide an interesting additional data point on the effect of stimulus-onset asynchrony on the N400 semantic priming effect. Testing four different stimulus-onset asynchronies (200 msec, 400 msec, 600 msec, 800 msec) we found no significant effect of stimulus-onset asynchrony on the size of the N400 semantic priming effect, consistent with previous ERP research demonstrating N400 effects of similar sizes across short and long SOAs (Anderson & Holcomb, 1995).

5. Conclusions

We used a novel semantic priming paradigm in MEG to investigate whether temporal predictability plays a critical role in the robust facilitatory effects of semantic predictability observed in the N400 response during language comprehension. We found that semantic predictability effects were not larger in the presence of temporal predictability. Our results suggest that, at least for visual word presentation, ‘predicting when’ may make little contribution to the benefits derived from ‘predicting what’ at the lexical-semantic level, and these data may provide clues to the mechanisms supporting contextual predictive facilitation in language comprehension.

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